FACTORS THAT AFFECT NATURAL REGENERATION, GROWTH, AND SURVIVAL RATES OF THREATENED AND ENDANGERED SPECIES IN DRYLAND FORESTS IN HAWAI'I.

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CHAPTER 1

INTRODUCTION

Globally, tropical dry forests represent more than 40% of tropical forests (Ceccon et al. 2006; Murphy and Lugo 1986). Dry forests are most commonly defined by the length of the dry period – which usually extends over several months - rather than the annual precipitation (Miles et al. 2006). They also typically (Hawai‘i is an exception) harbor many species that are deciduous during the dry season, which is an adaptation to seasonality and drought (Miles et al. 2006). Tropical dry forests have an annual precipitation between about 400 and 1700 mm (Ceccon et al. 2006; Gerhardt and Hytteborn 1992) and there is a greater variation in annual rainfall or "pulses" than there is in other forest ecosystems. Tropical dry forests differ in diversity, species composition, function, and structure and as Gerhardt and Hytteborn (1992) explain, "there is a large variation among the forests which occur in the areas between the evergreen tropical rain forests and the dry savannas and deserts".

Tropical dry forests once covered more than half of the world's tropics (Murphy & Lugo, 1986; Brown & Lugo, 1982) but today are the most threatened of all major lowland tropical forest habitats (Miles et al. 2006; Olson and Dinerstein 2002; Janzen 1988). Globally, they are exposed to similar threats such severe large-scale changes due to deforestation, establishment of pastures, and more intense and frequent fires; both accidental and intentional (Swaine 1992). Tropical dry forests are one of the biomes most threatened by deforestation and conversion to agriculture (Maza-Villalobos et al. 2011; Sanchez Azofeifa et al. 2005; Miles et al. 2006). These areas continue to support larger human populations than the more wet forest areas. For example, in Central America less than 2% of dry forests are intact and less than 0.1% of the original forests, which once covered an area the size of France, have any kind of conservation status (Janzen 1986, 1988) and are in relatively low pristine condition (Janzen 1986a). Dry forests in Costa Rica have experienced decades of logging, burning, and clearing for pastures and agriculture which have reduced them to fragments ranging in size from a few hundred hectares to areas with only a single tree remaining. Other tropical dry forests occur in southern Mexico, Bolivia (Bullock et al., 1996; Gentry, 1993; Parker et al., 1993), northwestern South America (Bullock et al., 1996; WWF/IUCN, 1994; Parker & Carr, 1992), the sub-tropical forests of Maputaland-Pondoland in south-eastern Africa (Cowling & Hilton-Taylor, 1994), Madagascar,

and New Caledonia which also possess a high number of endemic taxa (Wikramanayake et al., 2001).

Tropical dry forests on small islands have biota that are highly vulnerable or critically endangered due to their limited habitat and ranges, and their sensitivity to anthropogenic/natural disturbances and invasive species (Olson and Dinerstein, 2002; Brooks et al., 1997; ReakaKudla et al., 1997; Sujatnika et al., 1995; WCMC, 1992; Raven, 1988; Wilson, 1988, 1992). These include, Caribbean dry forests which are susceptible to annual hurricane disturbances and have become highly threatened due to the destruction of their forest structure over a longer time scale (Imbert and Portecop, 2008). Island ecosystems, especially those of tropical dry forest habitats, are projected to experience greater extinctions over the next two decades on account of the sensitivity and high endemism, and the extensive threats that native species must face (Olson and Dinerstein, 2002).

Although dry forests are found throughout the world, Olson and Dinerstein (2002) state that tropical dry forests are widely overlooked and that losing these ecosystems would be an enormous loss of global biodiversity and requires immediate conservation action. Restoration of dry forests has become even more difficult since there is very little knowledge of reference or benchmark habitats to help guide this effort (Janzen 1988). With limited funding, conservation managers are forced to rely on strategic methods that allow for effective results while using the smallest amount of resources to protect high areas of biodiversity.

As with other tropical dry forests around the world, Hawai‘i’s dryland forests are one of its most culturally important and most severely endangered and exploited habitats (Miles et al. 2006; Olson and Dinerstein, 2002; Cabin et al. 2001; Janzen 1988; Murphy& Lugo 1986). Like elsewhere in the tropics, Hawai‘i’s dry forest regions were the first to be settled and their resources the first to be consumed. This is mostly because these areas were the most hospitable in terms of climate, and offered fertile soil and obtainable resources (Allen 2000). According to the Ka‘ūpūlehu Dryland Forest Preserve in North Kona, “The native dry land forests were a bountiful source of diverse plant materials used for tools, vessels, food gathering, fishing, shelter, medicines and rituals” (HFIA, 2007). This gave Hawaiians a suitable environment to live in, where one could be close to the ocean but also to the mountains, while still inhabiting a site that was easily accessible to materials for everyday life and survival. Nearly everything that could be attained from the rain forest could be found in the dryland forests and the forests were a source

of a wide variety of tree species that contributed wood to early Hawaiians, who, without metal, viewed dryland forests as a source of abundant hardwoods (Medeiros et al 1998).

Today, it is estimated that less than 10% of Hawaiian dryland forests remain, with some estimates as low as 3% (Gillespie et al. 2011; Cordell et al. 2002; Cabin et al. 2000). More than 25% of the officially listed threatened and endangered Hawaiian plant species are endemic to dry forest habitats (Cabin et al. 2001; 2002; Blackmore and Vitousek, 2000; Bruegmann, 1996) and all remaining dry forests in Hawai‘i have the highest number of endangered species of any habitat (Sakai et al. 2002). This represents a great decline in biodiversity, since in the past these forests were once described as the most diverse in the Hawaiian archipelago. Joseph F. Rock identified Hawai‘i dry forests such as Auwahi District on Maui and Pu‘u Wa‘awa‘a District on Hawai’i Island as the richest botanical regions in the territory, with more tree species than any Hawaiian rain forest (Rock, 1913).

With the introduction of ranching in the mid-1800’s, degradation and deforestation of Hawaiian dry forests originally occurred on leeward slopes between 1200 and 2200 m elevation (Cuddihy & Stone 1990). This prompted more frequent fires linked with agriculture. The introduction of the Pacific rat (*Rattus exulans*) brought by the Polynesians (Wilmshurst et al. 2011; Athens 2009) also helped expedite forest decline due to heavy rates of seed predation (Cordell and Sandquist 2008; Blackmore and Vitousek 2000; D’Antonio and Vitousek 1992; Cuddihy and Stone 1990). These direct impacts have also been intensified by indirect effects such as the loss of species such as birds and insects that once performed critical ecological services such as pollination and seed dispersal and scarification (Giffin, 1993; Olson and James, 1982).

West Hawai‘i has some of the best dry forests remaining in Hawai‘i but there is still little information on if natural regeneration.is occurring in restored areas and what factors most affect the growth and survival of naturally recruiting dry forest species. According to Friday (2015), “Although native plant species regenerate passively (i.e., without outplanting or invasive species control) in some cases, particularly where the original forest has only recently been degraded (e.g. Scowcroft et al. 2008), forests in Hawai‘i generally have been degraded so long and invasive species (particularly grasses) are so abundant that there is little passive native regeneration”. Previous studies have indicated that seedling regeneration has very little success without the exclusion of ungulates as well as the removal of alien plant species (Weller et al.

2011; Cabin et al. 2000). Most of the understory in North Kona region is dominated by nonnative grasses such as African fountain grass (Pennisetum setaceum), an alien perennial bunch grass first seen in the Hawaiian Islands in 1914 (Jacobi and Warshauer, 1992) and which has had a big impact on regeneration. Fountain grass cover leaves few native seedlings to establish themselves or even recruit into larger trees (Litton et al. 2006; Cabin et al. 2000; D'Antonio et al. 1998; D'Antonio & Vitousek 1992).

Today protected areas of dry forests in Hawaiʻi including Kaʼūpūlehu, Puʻu Waʻawaʻa, and Auwahi (on Maui) have focused on removing the biggest threats to dry forest - fire, ungulates, and invasive grasses - for more than 15 years. But even with these threats removed, there is little information on if natural regeneration is now occurring and on what other factors may most support regeneration of threatened and endangered species: what is the success of regeneration from wild and outplanted species in these areas and what are the main factors that allow for it? If there is regeneration, it is also essential to understand if it is sufficient to maintain populations over the long-term – therefore to understand and project the long-term dynamics of populations (Crone et al. 2011).This study was a collaboration with managers at two dryland forest restoration projects on Hawaiʻi Island, Kaʻūpūlehu dryland Forest and Puʻu Waʻawaʻa Forest Reserve to address the following questions: (1) Is natural regeneration of threatened and endangered species occurring? and if so (2) What are the rates of survival and growth of naturally regenerated T&E species selected species over time?

Study Sites

Kaʻūpūlehu Preserve

The Kaʻūpūlehu Preserve is located on the west side of the Big Island in North Kona district on Hualālai Mountain where it covers about 31 hectares (Thaxton et al., 2010) at about 600m elevation (Cordell et al. 2008) (Figure 1.1). It is part of the ahupuaʻa of Kaʻūpūlehu, which extends from the summit of Hualālai to the ocean. It was established in 1999 (fenced in 2000) and it is owned by the largest private land-owner in Hawaiʻi, Kamehameha Schools (King and Roth, 2006). Management consists of ungulate control/fence maintenance, invasive plant removal, fire mitigation, native plant restoration, and educational outreach. Since its establishment, thousands of plants have been outplanted in the fenced preserve on rough lava terrain. The site is dominated by two distinct substrates (which act as natural fuel breaks) where the most recent lava flow occurred in 1801 (Kauahikaua et al. 2002) and the older substrate consists of flows dating back 750 years (Wright et al. 1992). Lama (*Diospyros sandwicensis*) is the dominant species of the older substrate, and ʻŌhiʻa is the dominant species of the younger substrate.

Rainfall for Kaʼūpūlehu ranged from 1249 mm in 2004 to 122 mm in 2012, with a mean of 527 ± 301 mm (Figure 1.2). Rainfall for the period of this study (2015-2017) was higher than the 20-year average, but at or below the 92-year average extrapolated from the Hawaii Rainfall Atlas - 714± 291 (Giambelluca et al. 2013). Frazier et al. 2017 have showed that rainfall in North Kona has decreased by 6-8% per decade since 1920.

Over the years the forest preserve has gone through multiple changes and challenges in terms of the introduction of alien species of plants and herbivores, long periods of drought, fire, and increasing human habitation. Early studies suggested that even with successful methods in eliminating ungulates and invasive species, the natural regeneration of native species has not met the desired standards (Thaxton et al., 2010; Cabin et al. 2000; Stratton et al., 1998). However, in recent years, resource managers have observed regeneration success and there is a need to understand the rates of success and the factors that have allowed for this. Kaʼūpūlehu has over 10 species that are federally listed as threatened or endangered, and some are PEP species (plants with fewer than 50 individuals in the wild or for which wild founders are extinct (Table 1) and

managers of the preserve have some records of natural regeneration of these species since 2004 as well as records for outplants of these species since 2007.

Despite its small size of about 31 ha, this preserve remains one of the best native dry forest remnants left in Hawai‘i (Cabin et al., 2000). Not only is Ka‘ūpūlehu dryland forest rich in plant diversity but is rich with sacred sites and historical artifacts, showing how people and place are heavily connected. Some of the lineal descendants who have lived in Ka‘ūpūlehu for years, and still work there today, have helped preserve its dry land forest and cultural significance for future generations.

Pu‘u Wa‘awa‘a Forest Reserve

The Pu‘u Wa‘awa‘a reserve is part of the ahupua‘a of Pu‘u Wa‘awa‘a where it is located on the west side of the Big Island and lies on the northern flank of Hualālai mountain where it is bound between the 1859 lava flow from Mauna Loa and the 1800-1801 Ka‘ūpūlehu lava flow from Hualālai (Figure 1.4). Pu‘u Wa‘awa‘a is located in a moderately dry moisture zone (Figure 1.3). Precipitation depends on the elevation, but the average precipitation between 1938-1974 at 1000 meters was 1186.2 (Price et al. 2012; Griffin, 2003).

The area is marked by a prominent landmark of a volcanic vegetated cinder cone and the whole region was forested with native vegetation in the past but has been disturbed and decimated by wildfires and more than 100 years of grazing livestock. In 1848 Kauikeaouli, King Kemehameha III, claimed the ahupua‘a of Pu‘u Wa‘awa‘a as his own lands but set aside some land to the Kingdom that would help support government activities. When the monarchy was overthrown in 1893, these lands were later converted into pasture and ranch lands where about 14,000 goats, cows, and sheep were raised on 105,831 acres (Griffin, 2003). After the sheep wool industry was abandoned, the State of Hawai‘i retained these lands and the State Board of Land and Natural Resources established the Pu‘u Wa‘awa‘a Forest Bird Sanctuary (PWWFBS) in 1984. Management was later transferred from the State’s Land Division to the Division of Forestry and Wildlife (DOFAW) where their main objective was to preserve 3,806 acres of habitat for endangered forest birds because of concern of habitat loss after the result of illegal Koa harvesting activities. The remaining land that was not portioned off for the bird preserve was leased to a private owner who created the Dillingham Ranch Inc. business for 40 years until 2000. Once the lease expired, the area was transferred to DOFAW and State parks with aims to

restore native plant and animal ecosystems, to preserve culture resources, reforestation, public hunting and recreation, pasture management, and future research (Griffin, 2003).

As with all dryland forests, drought is a challenge and non-native grasses and weeds continue to compete and take over native understory plants (Cordell et al., 2008). As with Kaʻūpūlehu, Puʻu Waʻawaʻa is managed to prevent fires and control invasive species, and ungulate grazing within protected units. In 1988 and 1995 the area experienced large wildfires that have left scars to this day and has created a major impact to the native dryland ecosystem since the forest has continued to experience repeated burns in the last few decades.

Even though the area has gone through many alterations over the past 100 years, there are remnants of intact forests that still endure. Close to 182 native species in 69 families grow in Puʻu Waʻawaʻa (Griffin, 2003). Today its forests are primarily dominated by Lama (*Diospyros sandwicensis*), ʻOhiʻa lehua (*Metrosideros polymorpha*), Alaheʻe (*Psydrax odorata*), Wiliwili (*Erythrina sandwicensis*), Ohe makai (*Polyscias sandwicensis*), and Kauila (*Colubrina oppositifolia*). Endangered species that can be found in the area include Maʻo hau hele (*Hibiscus brackenridgei* spp. *brackenridgei*), Uhiuhi (*Mezoneuron kavaiensis*), Kokiʻo (*Kokia drynarioides*), and Halapepe (*Chrysodracon hawaiiensis*).

With these remnants of dryland forests remaining, managers at Puʻu Waʻawaʻa share very similar concerns and objectives to those at Kaʻūpūlehu dryland forest preserve. Resource managers at both sites hope to improve our understanding of the regeneration and viability of T&E populations.

MATERIALS AND METHODS

Study Species

The 11 threatened an endangered species that we studied were Koʻo loa ʻula (*Abutilon menziesii*), Koʻo lau (*Bidens micrantha* subsp. *ctenophylla*), Bonamia (*Bonamia menziesii*), Halapepe (*Chrysodracon hawaiiensis*), Kauila (*Colubrina oppositifolia*), Maʻo hau hele (*Hibiscus brackenridgei* spp. *brackenridgei*), Hau kuahiwi (*Hibiscadelphus hualalaiensis*), Aupaka (*Isodendrion pyrifolium*), Hau hele ʻula (*Kokia drynarioides*), Uhiuhi (*Mezoneuron kavaiensis*), and Maʻaloa (*Neraudia ovata*) (Table 1). These were identified as high priority by reserve managers.

Table 1.1. Study Species. All are threatened or endangered according the Endangered Species Act (ESA). PEP (Plant Extinction Prevention Program) species are those with < 50 individuals in the wild or with no wild founders.

Scientific Name	Common Name	Family	Species Code	PEP	Presence of wild adults in Ka‘ūpūlehu Preserve	Year Outplanted in Ka‘ūpūlehu Preserve
Abutilon menziesii	Ko‘o loa ‘ula	Malvaceae	ABUMEN	N	No	2002
Bidens micrantha* subsp. *ctenophylla	Ko‘o lau	Asteraceae	BIDMIC	N	No	2002
Bonamia menziesii	Bonamia	Convolvulaceae	BONMEN	N	No	1999
Chrysodracon hawaiiensis	Halapepe	Asparagaceae	CHRHAW	N	Yes	2000
Colubrina oppositifolia	Kauila	Rhamnaceae	COLOPP	N	Yes	1999
Hibiscus brackenridgei* subsp. *brackenridgei	Ma‘o hau hele	Malvaceae	HIBBRA	Y	Yes	2001
Hibiscus hualalaiensis	Hau kuahiwi	Malvaceae	HIBHUA	Y	Yes	2003
Isodendrion pyrifolium	Aupaka	Violaceae	ISOPYR	Y	Yes	2010
Kokia drynarioides	Hau hele ‘ula	Malvaceae	KOKDRY	Y	Yes	1999
Mezoneuron kavaiensis	Uhiuhi	Fabaceae	MEZKAV	N	Yes	1999
Neraudia ovata	Ma‘aloa	Urticaceae	NEROVA	Y	No	NA

Monitoring Recruitment, Survival, and Growth

We identified all naturally regenerated individuals of all eleven-study species, across the restored portion of Kaʻūpūlehu Preserve (Figure 1.5) or three years (2014-2017). Specifically, to determine survival, growth and regeneration of natural recruits, we tagged and measured all newly recruited individuals of our 11-study species in Kaʻūpūlehu Preserve in December 2015, 2016 and 2017. We were also able to utilize results from a previous census carried out in 2013. For each plant >10cm height, we recorded species name, height (from the ground to the top of the apical meristem), diameter at breast height (when relevant), basal diameter, distance to the presumed parent plant, parent tag ID, survival status, observations of health (including intensity of herbivory), presence of flowers and/or fruit, and GPS waypoints. Photos were also taken to visually document growth over time. We were unable to identify the source of about 14% of the recruits. For Puʻu Waʻawaʻa, we used the same methods but only monitored once per year in the summer (2016-2017). We remonitored in four separated fenced units which include: Hauaina Unit, Oweowe Unit, Unit III, and Uhiuhi Unit.

Each naturally regenerated plant was given their own ID number marked with a tag. Tags consisted of metal aluminum marking tags which were tied around a flag and placed at the base of each seedling. Given that there were hundreds of Koʻo lau recruits we counted all recruits in each patch, and then tagged two randomly selected recruits per patch to monitor growth and survival. Similarly, for Aupaka, to avoid stepping on and damaging plants, we counted all recruits in each patch and for each group of three plants we tagged only one.

RESULTS

Number of Natural Recruits

Over all species, there was an increasing trend in the total number of recruits over time in Ka'ūpūlehu (Figure 1.6a), with a total number of 292 recruits found in 2017. We found new seedling recruitment for all of our study species, but the number varied widely across species (Figure 1.6b). The total number of naturally recruited individuals ranged from 55 - 292 recruits per species in a given year and was highest for Kauila, Maʻo hau hele, Uhiuhi, and Bonamia. Hau kuahiwi, Koʻo loa ʻula, Hau hele ʻula, Halapepe, and Maʻaloa had the lowest numbers of recruits (Figure 1.6b). Only one individual recruit was found for Hau kuahiwi. The majority of species showed an increasing trend over time; the exceptions were Uhiuhi and Hau hele ʻula species. For Puʻu Waʻawaʻa, we observed natural recruitment in all four fenced units but only two species were found Hau hele ʻula than Maʻo hau hele (Figure 1.6c). There were more natural recruits for Hau hele ʻula (56) than Maʻo hau hele (32) in 2016, but by 2017 both species showed similar numbers of natural recruits (32 and 33 respectively; Figure 1.6c).

In terms of the number of new recruits produced per year, Uhiuhi, Maʻo hau hele, and Kauila produced the highest numbers, up to 50 recruits in one year for Uhiuhi (Figure 1.7a). Overall, Koʻo koʻo lau had the highest number of new recruits with about 1246 recruits found in 2017 (This is not included in Figure 1.7a. since the number was so much higher than that of the other species). At Puʻu Waʻawaʻa, Maʻo hau hele also produced more natural recruits (12) than did Hau hele ʻula (4).

The number of natural recruits can depend on the number of reproductive adults present. Based on our data from 2017, Uhuhi and Aupaka produced the most recruits per reproductive adult, followed by Maʻo hau hele (Figure 1.8). Both Halapepe and Hau hele ula had many reproductive adults but produced very few seedlings.

Source of Natural Recruits

At Ka'ūpūlehu, when we identified the source of recruits and found that about 76% of recruits came from outplanted sources, while the rest came from wild sources (Figure 1.9a). When looking at each species (Figure 1.9b) we found that all, or he vast majority of recruits from Halapepe, Kauila, and Uhiuhi came from wild sources. This makes sense since a majority of

Kupuna or wild trees that make up Ka'ūpūlehu forest are of these three species and the outplants are just starting to flower and fruit. For Aupaka, Koʻo koʻo lau, Maʻaloa, Maʻo hau hele, Hau hele ʻula, and Hau kuahiwi, 100 % of the new recruits come from outplants. For Koʻo loa ʻula about 1/3 are from wild sources while about 2/3 are from outplanted sources.

Rates of Survival, Growth, and Reproduction

In Kaʻūpūlehu Preserve, overall annual survival of naturally regenerated recruits of all species combined ranged from 73% - 80%, with 2015-2016 having the lowest survival and a 2016-2017 the highest (Figure 1.10a). By species, Uhiuhi and Hau hele ʻula had the lowest survival while Kauila, Aupaka, Maʻo hau hele, and Halapepe had the highest survival (Figure 1.10b). Uhiuhi and Hau hele ʻula had heavy rates of insect herbivory. At Puʻu Waʻawaʻa, survival was also higher for Maʻo hau hele (65.5%) than for Hau hele ʻula (50%) in year 2016 - 2017 (Figure 1.10c). Breaking up survival by size (Figure 1.10d), survival of small individuals (<50cm high) was lower than that of larger ones (>=50cm) for Uhiuhi and Hau hele ʻula. In most years there were < 4 Koʻo loa ʻula and Halapepe small recruits, and <4 Hau hele ula and Halapepe larger recruits. The lack of data for small Koʻo koʻo lau individuals is a reflection of our tagging system – there were hundreds of small recruits but we did not tag them.

Across years and sizes at Kaʻūpūlehu Preserve, growth (change in height) of natural recruits was greatest for Maʻo hau hele and Aupaka. Overall for plants less than about 150 cm high, growth was lower in 2015-2016 than in the other two years (Figure 1.11). In 2015-2016 Uhiuhi and Koʻo loa ʻula showed negative growth (die back) (Figure 1.11b). The tallest natural recruits for trees were for Maʻo hau hele and Kauila (up to 3.5 and 4 m respectively) (Figure 1.11).

Kaʻūpūlehu Preserve, flowering and fruiting was observed in Winter (November/December) on naturally regenerated recruits of Aupaka, Bonamia, Kauila, Koʻo koʻo lau, Koʻo loa ʻula, and Maʻaloa (Figure 1.12). In terms of the trees, Kauila had very high percentage of recruits flowering or fruiting (66.7%) and an increase in the percentage of individuals flowering over time from 2014 to 2017 . In contrast, no Uhiuhi were large enough to flower. For shrubs, Koʻo koʻo lau and Maʻaloa had the highest percentage of flower or fruit (16.2% - 59.2% ± 19.5%), while Aupaka, which had recently started to regenerate naturally, had the lowest percentage. For vines, Bonamia flower or fruit was not observed in year 2017 but was

observed in previous years. We recorded flowering and fruiting only in December and so species that flowered or fruit at other times are not included.

DISCUSSION

Naturally Regenerated Keiki

Previous studies have shown that the exclusion of ungulates and removal of alien plant species can have a significant positive effect on native plant regeneration and growth in Hawai‘i (Cabin et al. 2000; Weller et al. 2011). The recovery of forest species in areas such as abandoned neotropical pastures is dependent on the dispersal of new seeds from nearby forest remnants (Holl et al. 2000) and that also can affect regeneration. It has also been shown that root systems of many invasive grasses are dense and can restrict nutrient and water uptake by native species, and dense above-ground grass biomass inhibits both germination and growth of natives (Soriana & Sala 1983; Gordon, Menke & Rice 1989; D’Antonio & Vitousek 1992; Cabin et al. 2002a, b; Cordell et al. 2008). In the Auwahi dry forest restoration project on Maui, shrub nurse plants and the establishment of a shrub understory have had the strongest benefits on regeneration of native tree species including enhanced germination and seedling survival (Medeiros, 2006).

Dry forest remnants such as Ka’ūpūlehu have had fenced enclosures and ungulate-free for over 15 years with intensive weed management and are predominantly covered with native species. However, previous studies have documented little natural recruitment (Cabin et al. 2000, Cabin et al. 2002, Brooks et al. 2009). In contrast, our research documented the presence of natural recruits for all of the 11 T&E species we studied, and an increasing number of naturally recruited individuals for most of these species, except for Hau hele ‘ula and Halapepe. Koʻo koʻo lau, Maʻo hau hele, Kauila, Bonamia, showed especially high levels of natural recruitment by 2017. One of the most impressive recoveries was Koʻo koʻo lau, where we documented over 1000 recruits and sometimes as much as 100 in one 1x1-meter plot. This species is wind dispersed and grows quickly, and has a short lifespan, which may account for why there were so many recruits. Similarly, in Nicaragua dry forests, seeds that were wind dispersed predominated in the mature forest and in early successional stages (Sabogal 1992; Ceccon et al. 2006). A second remarkable recovery, so far at least, is the critically endangered Aupaka, which has gone from no observed recruits in 2013 to 37 recruits in 2017, including those that were flowering and

fruiting. The successful recruitment across most species is likely due to the weed management program at Ka'ūpūlehu combined with the succession of the forest.

In terms of the species that are not recruiting well, halapepe is common in the area due to outplanting (Table 1), and we observed abundant fruit production over our study period. Hau hele ʻula was described by Cabin et al. (2000) as one of the most abundant fruiting species in Ka'ūpūlehu in 2000 and although most of the wild plants have died, due to outplanting, this species is abundant today too, with many individuals producing fruit. Low regeneration these and other species may be in part a result of the decline of forest bird populations (Sakai et al. 1988, Blackmore & Vitousek 2000, Ziegler 2002, Pratt & Jacobi 2009; Tagawa 2013) and which may have served as pollinators or dispersers. Understanding patterns of pollination and seed dispersal can play an important role in understanding the fecundity and seed survival and ultimately the lack of regeneration (Loiselle & Blake 2002, Kirika et al. 2008). Disruptions to plant-animal mutualisms can negatively affect the stability of plant populations (Willson & Traveset 2000, Traveset & Richardson 2006, Rodriguez-Cabal et al. 2007) and this can be true especially in Hawaiian dry forests since 76 percent of native trees have fleshy fruits adapted for bird dispersal (Wagner et al. 1999, Pau et al.2009). The diverse native avifauna that dry forests supported before human arrival (Olson & James 1991) has now been replaced by introduced birds especially in dryland forests (Pratt et al. 1987). Chimera and Drake (2010) found that smaller birds such as the Japanese white eye overwhelmingly prefer consuming smaller seeds which enable those plants with smaller seeds to have a higher chance of reproducing. Hau hele ʻula, Uhiuhi, and Halapepe seeds are large and not likely able to be dispersed by anything today.

In dry forests, dispersion of seeds occurs mainly during the dry season and seeds remain on the forest floor until the next large rain event when favorable conditions are met for germination (Ceccon et al. 2006). Those seeds that are not able to be dispersed by extinct avifauna are also prone to predation by other introduced mammals such as the rat (Rattus exulans, *Rattus rattus*) and house mouse (Mus musculus) (Chimera and Drake 2011). The Hawaiian Archipelago lack native rodents (Drake and Hunt, 2009) and introduced rats are a key contributor to both historical and current forest degradation (Medeiros et al. 1986; Cabin et al. 2000; Athens et al. 2002; Athens 2009; Meyer and Butaud 2009; Chimera and Drake 2011). The pattern of rat predation drastically changing lowland forests is seen throughout all island ecosystems that have introduced rats (Athens 2009).

In Ka'ūpūlehu, rodent control is being applied but in only certain areas. Kauila seeds are predated by rats - we have observed bite marks on seeds surrounding parent trees - and this may be why Kauila recruits are found farther from the parent plant rather than directly underneath, where the majority of seeds fall and may be more heavily predated (Janzen 1988). Chimera and Drake (2011) studied predation of seeds of three dry forest species on Maui, including a different species of Halapepe (*Pleomele auwahiensis*) and showed that significantly more seeds were removed under parent trees than in exposed areas away from trees. Although we did not observe predation on Halapepe or Hau hele ʻula seeds in Ka'ūpūlehu these are also highly predated by rats. We observed birds feeding on Halapepe fruits, which have fleshy exteriors, but the hard-interior seed is still left intact on the parent plant which suggests that there are no large bird dispersers that can consume the whole seed.

For some recruits it wasn't possible to identify a nearby parent plant and these may have been dispersed by birds. In Puʻu Waʻawaʻa, Erckel's Francolin birds (*Francolinus erckelii*) were observed to dig around Maʻo hau hele roots, damaging roots but perhaps also suggesting that these birds may be dispersers for this species as has been reported for other native species (Chimera and Drake 2011). The fact that we only observed Hau hele ʻula and Maʻo hau hele in Puʻu Waʻawaʻa could be due to multiple factors, including the numbers of reproductive adults, and the fact that Puʻu Waʻawaʻa exclosures are managed less intensively for weeds than in Kaʻūpūlehu.

Many tropical forest seeds are short-lived and are often not viable in the ground for long periods (Garwood 1989; Ceccon et al. 2006). Some species that fruit in the dry season may form a short-lived seed bank until the rainy season (Foster, 1982; Garwood, 1982), while other species may have long-lived seedbanks. However, seed banks may play a reduced role in regeneration if droughts are prolonged (Skoglund, 1992; Rico-Gray and Garcia-Franco, 1992; Miller, 1999). Seed banks also may have high seed mortality due to environmental stress, limited dispersal, predation, and restrictions in germination during favorable conditions (Ray and Brown 1994; Ceccon et al. 2006). The only species we observed geminating from a seedbank was Uhiuhi since there are no outplant reproductive adults.

Survival and Growth of Recruits

We found high survival rates for a majority of the species we monitored. Overall annual survival ranged from 73% - 80% percent over the three-year study period. The higher survival we observed as compared to previous studies of outplants (Cordell et al. 2008) may be a result of changing microhabitat, as the forest canopy fills out and there are changes in the soil microbiota, and/or because natural recruits germinate and survive in those places that are most suitable. It should also be taken into account that over the three-year study, rainfall was a little over the average. However, in both studies, Uhiuhi had similarly very low survival rates which suggests that this species has had low survival for many years.

Negative growth rates for Uhiuhi and Koʻo loa ʻula in 2015-2016 was due to die back and resprouting. Both Uhiuhi and Hau hele ʻula had high rates of mortality of the seedlings and both had high levels of insect herbivory. For Uhiuhi in particular, this is due to ant and mealy bug interactions (Styrsky and Eubanks, 2007; Jahn and Beardsley, 2000), which infest stem and roots of Uhiuhi. As a result, Uhiuhi seedlings tend to fall over once they get to a certain height (about 40-50 cm). This is why they showed a decrease in maximum height over time. In Hawaiian dry forests, precipitation can be very variable over time. Uhiuhi had the highest number of recruits in year 2015 which had the highest amount of annual rain in the three years we remonitored, suggesting that water availability may influence germination for this species. The other factors such as insect herbivory, light availability, that may affect survival and growth are discussed in Chapter 2.

One troubling occurrence in dry forests in Hawai'i is the reproductive deficiency of native tree species (Loope 1998, Cabin et al. 2000, Chimera and Drake 2010). Janzen (1988) refers to trees that fail to reproduce as 'the living dead,' and proposes that this problem is typically found in tropical dry forests worldwide. We found that for tree species, Kauila natural recruits greater than 1.4 m size produced fruit and flowers. All of the shrub species were at least starting to produce flowers and fruit, as did the vine, Bonamia. This suggests that for most of the species we monitored, naturally regenerated individuals are able to grow to reproductive maturity and produced seeds. Since we only monitored once per year, we were not able to obtain full information on flowering and fruiting for Maʻo hau hele and Hau hele ʻula natural recruits.

Recommendations for Management

Identifying strategies for what works best for dry forest restoration heavily depends on understanding each forest area and its forest dynamics. Challenges can range from the forest level to the species level. Goals for each area vary and resource managers may have different definitions of what success means to them. Fencing for predators locally, though costly and laborious, would have positive effects on native plant and native bird populations (Innes et al. 2012). Promoting mutualistic native to non-native species interactions (pollination and seed dispersal) could additionally help with restoring ecosystem function as seen in other studies (Cole et al., 1995, Foster and Robinson 2007). Climate change should also be considered when creating future management plans since a drying climate may negatively impact recruitment and survival.

The low recruitment observed for species like Hau hele ʻula and Halapepe suggest that a continuation of intensive outplanting is needed as are strategies to increase germination, including management for reduced seed predation and or hand dispersal. For Uhiuhi and Hau hele ʻula, efforts to control the ants and other insects will be important. It would also be useful to gain a better understanding of the role of mycorrhizae on native plant root systems as well as nutrient uptake in Hawaiian dry forests. Gemma et al. (2002) have shown that endemic and endangered Hawaiian species depend on mycorrhizae for nutrients and that those plants inoculated with the mycorrhizal fungi were 2.1-7.0 times larger than non-inoculated plants. All of the species tested were species typically found in dry and mesic forests in Hawai'i suggesting that using Mycorrhizae in outplanted plants grown in the nursery may help increase their probability of survival.

CONCLUSION

Overall, our research shows that of the 11 T&E species we monitored in Kaʻūpūlehu, at least three species (Halapepe, Uhiuhi, and Hau hele ʻula) are in need of further management to ensure continued regeneration. Two species (Hau kuahiwi and Koʻo loa ula) need further study for evaluation since the outplants by and large haven't reached reproductive maturity. But the other seven species show strong signs of regeneration and reproduction and provide much hope that these species are on their way to recovery. Future monitoring is needed at Puʻu Waʻawaʻa to further understand regeneration for other T&E species as some of its enclosures are still in its early stages of restoration and succession. The success of natural recruitment seen at Kaʻūpūlehu forest preserve suggests the importance of not only intensive management techniques but that community engagement and management go hand in hand.

CHAPTER 2

INTRODUCTION

Arthropods are substantial contributors to herbivory in forests (Basset, 1991), and one of the most important selective influences in the evolution of plants is their susceptibility to herbivory (Coley, 1983). The effects of herbivores on native plants species have shown to depend on resource availability (Blumenthal et al. 2009). In habitats with low-resource availability, plant species often invest heavily in traits that are considered resistant to damage (Funk and Throop, 2010; Zhang and Jiang, 2006; Coley et al. 1985), resulting in slow growth rates.

In tropical forests, most of the damage from herbivory has been found to occur in younger and expanding leaves (Coley & Barone, 1996). The young leaves of seedlings have higher nutritional quality than mature leaves and are particularly vulnerable to herbivory (Coley & Barone, 1996). Species that expand their leaves during the dry season have fewer insect herbivores and are more likely to avoid damage. Herbivory also has a substantial impact on plant fitness by depressing growth and by reducing ability to compete (Coley & Barone, 1996). Franks et al. (2006) found that survival and growth of seedlings from introduced insect herbivores in Florida were ~50% lower compared to controls.

The Hawaiian Islands harbor many unique species of plants and animals, with about 90% of the flowering plants being endemic (Allison, 2003, Wagner et al., 1999). However, the Hawaiian biota is also considered discordant, with few fast-growing plant species and a low number of native arthropods (Gillespie & Roderick, 2002; Wilson, 1996). Insect herbivores in Hawaiian dry forests include twig borers, sapsuckers, and leaf eaters which reduce the vigor of plant species (Banko & Banko, 2009). McAuliffe et al. (2016) observed a higher variety of arthropods and higher levels of herbivory in native sites compared to non-native sites. In Hawai‘i, herbivores have also shown to threaten the seedlings of rare species. For example, Joe & Daehler (2008) found invasive slugs to threaten 59 rare plant species, reducing seedling survival more in endangered seedlings compared to non-endangered native and invasive seedlings. Gregg et al. (2018) showed that in Hawaiian dry forests, invasive social insects impair forest recruitment by damaging vegetation and altering ecosystem processes. The combination of both insect and disease can also impact recruitment in dry forests (Krist et al. 2014).

Shade and water are other factors that can have strong effects on growth and survival of seedlings and saplings and can exacerbate or decrease insect herbivory and its impacts. Water is a limiting resource in tropical dry forests and in Hawaiian dry forests, seedling regeneration is observed during periods of rain and when there is higher soil moisture (Cabin et al. 2000). Thaxton et al. 2012 showed that survival and relative growth rates of native dry forest species increase significantly with soil moisture (Thaxton et al. 2012). In Auwahi dry forest (Maui), restoring a forest is a vital part in reestablishing its soil hydrology. Perkins et al. (2012) compared a reforested area and adjacent grassland, and showed that reforestation increases hydraulic conductivity, preferential flow, and hydrophobicity, resulting in better distribution of infiltrated water faster and deeper, which is pertinent for native plant needs and health. However, Hawaiian dry forests areas have become drier over the last century (Frazier et al. 2017) and climate change projections show that precipitation is expected to decrease further (Giambelluca et al., 2013).

Light transmitted through the canopy can have profound effects on understory vegetation (Winn et al. 2013). In Hawaiian dry forests, Cabin et al. (2001) found that the biomass of native species was greater in inter-canopy plots (full-sun areas) compared to sub-canopy plots (beneath canopy areas). Denslow et al. (2006) looked at limitations to seedling establishment in Hawaiian mesic forests and found that under different canopy cover conditions, both canopy and understory cover reduced seedling establishment. In Costa-Rica, Gerhardt (1996) found that high light levels improved seedling growth during the wet season but had a negative effect during the dry season, since it caused desiccation. In temperate forests, growth and survival for tree seedlings varies as a function of gap size, with optimal gap sizes occurring at intermediate levels (Kern et al. 2012).

For the past 20 years efforts have been made to restore Hawaiian dry forests by removing the largest threats – invasive ungulates, invasive grasses and fire; and by outplanting with threatened and endangered (T&E) species. Today some T&E species are regenerating but little is known about the abiotic and biotic factors that most affect their regeneration. In this study, which was a collaborative project with Ka'ūpūlehu Preserve managers, we assess the effects of differences in light, water and insect herbivory on the growth and survival of five threatened and endangered (T&E) dry forest species identified as priority for resource managers. Specifically, we ask:

How does canopy openness, soil water potential and levels of insect herbivory affect the survival and growth of Kauila (*Colubrina oppositifolia*), Maʻo hau hele (*Hibiscus brackenridgei* spp. *brackenridgei*), Halapepe (*Chrysodracon hawaiiensis*), Hau hele ʻula (*Kokia drynarioides*), and Uhiuhi (*Mezoneuron kavaiensis*) individuals, including both wild regenerated individuals and outplants?

Study Site

Kaʻūpūlehu Dry land Forest

The Kaʼūpūlehu Preserve is located on the west side of the Big Island in North Kona district on Hualālai Mountain, where it covers about 31 hectares (76 acres) (Thaxton, 2010) at about 600m elevation (Cordell et al. 2008). It is part of the ahupuaʻa of Kaʻūpūlehu, which extends from the summit of Hualālai to the ocean. It was established in 1999 (fenced in 2000) and it is owned by the largest private land-owner in Hawaiʻi, Kamehameha Schools (King and Roth, 2006). Management was propelled by community members and the need to conserve endangered species found in the area such as Uhiuhi (*Mezoneuron kavaiensis*) and Hau hele ʻula (*Kokia drynarioides*) and to create plans to further their survival. Management consists of ungulate control/fence maintenance, invasive plant removal, fire mitigation, native plant restoration, and educational outreach. Since its establishment, thousands of plants have been outplanted in the fenced preserve on rough lava terrain dating back to the 1800s. The site is dominated by two distinct substrates (which act as natural fuel breaks) where the earliest lava flow occurred in 1801 (Kauahikaua et al. 2002) and the older substrate consists of flows dating back 750 years (Wright et al. 1992). Lama is the dominant species of the older substrate, and ʻŌhiʻa is the dominant species of the younger substrate.

Despite its small size of about 76 acres, this preserve remains one of the best native dry forest remnants left in Hawaiʻi (Cabin et al., 2000). Not only is Kaʻūpūlehu dryland forest rich in plant diversity but is bountiful with sacred sites and historical artifacts, showing how people and place are heavily connected. Some of the lineal descendants who have lived in Kaʻūpūlehu for years, and still work there today, have helped preserve its dry land forest and cultural significance for future generations.

MATERIALS AND METHODS

To assess the effects of insect herbivory, canopy openness and water potential on survival and growth of natural recruits and outplanted individuals of our study species, we chose a subsample of 11-20 individuals/species (depending on the number available) from the wild regenerated individuals (Chapter 1) and 10 individuals/species of outplants. We selected individuals that spanned a range of canopy openness and sites. Since T&E species were not outplanted over the past five years, the outplanted individuals were generally bigger than the naturally recruits.

We considered insect herbivory to be any consumption of the leaf, stem and/or bark, or roots. To quantify insect herbivory, we monitored individuals in the dry (December 2016) and in the wet (June/July 2017) seasons, and visually ranked herbivory intensity as 0 (no insect herbivory observed), 1 (leaf herbivory <10%), 2 (leaf herbivory <20% or ants/mealy bugs/aphids present), and 3 (leaf herbivory >20% and ants/mealy bugs/aphids present). Canopy cover was measured using a Nikon camera and 180-degree hemispherical lens in July 2016. Photos were taken beside at each plant on the left side facing north and direct sun was avoided as much as possible. Gap analyzer (version 2.0) was used to analyze photos and calculate canopy openness as the percentage of light transmittance. Since there are very few deciduous trees in the Kaʻūpūlehu forest, we did not expect canopy cover to change seasonally.

A Nitrogen gas pressure chamber was used to measure water potential in Mega Pascals (MPa). Out of the five species, only 3 species (Hau hele ʻula, Maʻo hau hele, and Kauila) were measured for the outplants and 2 species (Maʻo hau hele and Kauila) for the natural recruits. This is because Halapepe leaves were flat and lacked a petiole, and therefore not amenable to measurement with the pressure chamber. For Uhiuhi in general and Hau hele ʻula natural recruits, there were not enough individuals to measure and we didn't want to risk the survival of those remaining. Leaf samples (one leaf per plant) were collected at predawn (before sunrise or daily minimum) between 5:00am-7:00am and at midday (maximum sun radiance) between 12:00pm-2:00pm. Predawn measurements are an indication of soil water availability to a plant and maximum daily water status, whereas midday measurements indicate minimum daily water availability and maximum daily water stress. Collection of leaf samples took about 30 minutes and leaves were measured as soon as possible since the pressure chamber was too heavy to carry

over the rough terrain. Leaves that were mature and in direct sunlight were selected for measurements.

We tested the effects of insect herbivory, canopy cover and water potential on growth and survival over one year (2016-2017) for each species separately, using linear multiple regression models, where final height was the response variable and initial height was a co-variable. For survival models, we used a binomial error distribution. We also tested how insect herbivory and water potential varied as a function of species, canopy cover and plant height. For all models, we log-transformed values of height and canopy cover. Data for both outplant and natural recruit subsets were combined for each model to increase sample size. We used Akaike's information criterion (AIC) to determine whether to drop or retain a given fixed-effect term, retaining factors that reduced the AIC value of the model. Full models were reduced in a backwards stepwise process, sequentially dropping the fixed-effect term in the model that increased AIC the most. All analyses run using in R v. 3.2.4.

RESULTS

Over our one-year study period, all individuals of four of our species survived– the only mortality that was observed was for Uhiuhi, where 30.8% of individuals died. Therefore, we were only able to test the effects of our variables on this species. The best fit model showed that the only significant predictor of Uhiuhi survival was plant height (Coefficient = 0.22922, SE = 0.08373, t = 2.738, P = 0.0229).

In terms of growth, none of the best fit models included insect herbivory, canopy openness, or water potential (predawn and midday). For all species except for Halapepe, growth decreased significantly with initial size (Table 2.1).

Table 2.1. Estimated coefficients from multiple regression models testing the effects of initial size (height), insect herbivory, canopy openness and water potential on final size (height). Coefficients from best fit models are shown.

Species	Variables	Coefficient	Standard Error	t-value	P-value	Sample size (n)
Kauila	**Intercept**	**0.135**	**0.150**	**0.900**	**0.377**	**28**
	Initial Size	**-0.187**	**0.057**	**-3.262**	**0.003**	
Ma‘o hau hele	**Intercept**	**0.279**	**0.059**	**4.752**	**5.93e-05**	**30**
	Initial Size	**-0.170**	**0.065**	**-2.601**	**0.015**	
Halapepe	**Intercept**	**0.152**	**0.031**	**4.877**	**1.21e-04**	**20**
	Insect herbivory	**-0.058**	**0.044**	**-1.312**	**0.206**	
Hau hele ‘ula	**Intercept**	**0.533**	**0.082**	**6.495**	**7.39e-06**	**19**
	Initial Size	**-0.430**	**0.069**	**-6.174**	**1.34e-05**	
Uhiuhi	**Intercept**	**-0.015**	**0.340**	**-0.045**	**0.966**	**9**
	Initial Size	**-0.356**	**0.113**	**-3.150**	**0.0254**	

The level of insect herbivory on Ma‘o hau hele, Uhiuhi, and Hau hele ‘ula was significantly higher than that of Halapepe and Kauila (Figure 2.1, Table 2). Across all species, insect herbivory increased significantly higher canopy openness (Table 2.2).

Table 2.2. Estimated coefficients from multiple regression model testing the effects of species and canopy cover on level of insect herbivory. For species, significant p values are in reference to Halapepe, which had very low insect herbivory.

	Coefficient	Standard Error	t-value	P-value
Intercept	**-0.008**	**0.250**	**-0.034**	**0.973**
Hau hele ʻula	**0.992**	**0.251**	**3.939**	**1.42e-04***
Kauila	**0.312**	**0.233**	**1.337**	**0.184**
Maʻo hau hele	**0.948**	**0.233**	**40.52**	**9.33e-05***
Uhiuhi	**1.036**	**0.270**	**3.834**	**2.08e-04***
Canopy	**0.012**	**0.005**	**2.216**	**0.029***

Kauila had significantly higher water potential and had more variation between individuals than Maʻo hau hele and Hau hele ʻula for both predawn and midday in both the summer and winter (Figure 2.2; 2.3, Table 2.3). The difference in water potential between predawn and midday was greater for Kauila and Hau hele ʻula. than for Maʻo hau hele, which varied little between the two-time periods.

Table 2.3. Estimated coefficients from multiple regression model testing the effects of species on a) summer (July) and b) winter (December) water potential. Significant p values are in reference to Kauila.

a)

Variables	Coefficients	Standard Error	t-value	P-value	Coefficients	Standard Error	t-value	P-value
	Predawn				Midday			
Intercept	**2.234**	**0.081**	**27.70**	**2e-10***	**3.097**	**0.202**	**15.307**	**2e-16***
Ma‘o hau hele	**-1.304**	**0.113**	**-11.53**	**2e-16***	**-1.993**	**0.128**	**15.615**	**2e-16***

b)

Variables	Coefficients	Standard Error	t-value	P-value	Coefficients	Standard Error	t-value	P-value
	Predawn				Midday			
Intercept	**1.232**	**0.309**	**3.992**	**2.99e-04***	**2.141**	**0.067**	**37.931**	**2e-16***
Ma‘o hau hele	**-0.083**	**0.123**	**-0.680**	**0.501**	**-0.929**	**0.100**	**-9.279**	**1.26e-11***
Kauila	**0.454**	**0.135**	**3.369**	**0.002***	**0.171**	**0.096**	**1.771**	**0.084**

DISCUSSION

Growth and Survival

For all five species of our study species, the only significant predictor of growth in our models was initial height, where larger plants showed less growth than smaller plants. We did not detect a significant effect of insect herbivory, canopy openness, or water potential on growth. This may be a result, at least in part, of our small sample sizes. It could also indicate high tolerance for these stressors or the stressors may be too low intensity for growth to be influenced. The effect of summer predawn water potential on growth was marginally significant for Kauila, suggesting that further work with a larger sample size might be valuable. In terms of canopy, although we tried to span the range of canopy, our results might be due to the relatively little variation in canopy cover.

Survival was 100% for all of our study species, except for Uhiuhi, where the only significant predictor of survival was initial size, such that taller individuals had higher rates of survival than smaller ones Since there was only one outplant of Uhiuhi in our sample, the rest of our sample were natural recruits. We had expected to find that insect herbivory was a significant predictor of mortality because we noticed that most mortality was a result of ants and mealy bugs on the stems and roots. The ants excavate around the roots such that the seedlings fall over. Reasons for not detecting this here, or in our growth models, may be that we only monitored insect herbivory twice in the year, and/or that the scale we used to rank herbivory was too coarse to detect differences.

Differences in Insect Herbivory and Water Potential Across Species

Insect herbivores prefer some plant species over others (Barton 2013). We observed non-native insects: mealy bugs, leafhoppers, beetles, white flies, and spider mites, especially on the young leaves of individuals and found that insect herbivory was significantly higher on Maʻo hau hele, Hau hele ʻula, and Uhiuhi than on Kauila and Halapepe. We observed large numbers of leaf-chewing insects such as the Chinese Rose Beetle (*Adoretus sinicus*) at night and early mornings on the leaves and buds of Maʻo hau hele. The large amounts of nectar produced by Hau hele ʻula's large flowers also attract large quantity of ants which don't necessarily cause herbivory but are usually associated with tending aphids and mealy bugs that do more damage to

the plant itself (Zhou et al., 2012; Conry, 2010; Offenberg, J.,2001). As previously mentioned, Uhiuhi is predominantly affected by ants and mealy bugs.

The leaves of lack of herbivory on Halapepe may be due to in part to the leaf thickness, but this species is heavily affected by the Banana Moth (*Opogona sacchari*) at Puʻu Waʻawaʻa, where its larvae web the newest leaves together and eat the fresh growth and flowers (Elliot Parsons and Edith Adkins, in review; CPP, 2012). Large infestations of the banana moth have not occurred in Kaʻūpūlehu but preparation for its possible invasion to this site should be taken into account by consistent monitoring and extra efforts in outplanting. As with Halapepe, there was little insect herbivory observed for Kauila and the majority of herbivory was seen on seedlings. Kauila is mainly threatened by the black twig borer (*Xylosandrus compactus*) (Greco and Wright, 2015), but no signs of this insect were observed on the seedings and saplings.

Predawn measurements of water potential or PMS (plant moisture stress) typically range between 0.3 – 1 MPa, and individuals with a PMS measurement of 1 MPa or higher are considered limited in certain physiological processes (PMS instrument company, 2018). For midday, PMS measurements are expected to be >1 MPa and as the PMS increases from 0.5 MPa or higher, plants become more and more limited in their ability to grow as this is the range in which photosynthesis becomes reduced (PMS instrument company, 2018). Kauila and Hau hele ʻula exceeded 2 MPa at midday in both seasons, but these dry forest species appear to be able to withstand these conditions. Sandquist & Cordell's (2007) found lower MPa measurements for Kauila but the increase from predawn to midday that we found here was consistent with their findings. The fact that Kauila showed a greater difference than Maʻo hau hele in predawn versus midday measurements, for both summer and winter MPa than Maʻo hau hele was not expected: Kauila is a tree species and even smaller individuals may develop deeper roots allowing for smaller differences in water (predawn versus midday) than those of Maʻo hau hele which is a shrub. Overall, out results show that in a low resource environment dry forest species show plasticity between species and are able to tolerate high water potential with little change as water stress increases.

Challenges and Future Research

Our study shows some of the difficulties of working with T&E species, especially the limitation of small sample sizes. Future studies that are able to use larger sample sizes (especially with young outplants – something that was not possible in our study) and longer periods that include dry years may reveal more information. A more precise ranking system of insect herbivory that incorporates different insect guilds and more frequent measurements throughout the year would capture more accurate effects on plant species. Further studies could also asses how introduced insects affect dry forest species and how this differs between seasons. Lastly, as we had originally planned but were unable to do, it would be interesting to investigate how outplants compare to natural recruits in terms of their ability to withstand abiotic and biotic factors.

CONCLUSION

Restoration depends on many factors, including the site since not all dryland forests are the same even if they have the same range of species. We still have so much that we don't know about these habitats but we need to also predict how these forests may be affected by oncoming changes such as climate change, increased fragmentation, and increased loss of native pollinators/frugivores. These forests are complex and today they rely heavily on our help to keep their populations afloat. But the findings documented in this study demonstrate that there is some hope in that some threatened and endangered dry forest species are doing well and appear able to sustain themselves in a restored context (and without long period of drought). Continued monitoring, combined with population projection models (Crone et al. 2012) can also help foresee how species will do in the future under changing conditions. For those species that may not be doing so well, monitoring such as the kind we carried out can shed light on how we can adjust management plans/actions to enhance their populations such as planting more outplants, managing for insect pests, and planting combinations (combining the outplanting of two or more plant species that may grow well together) among others.

The high success of regeneration, survival, and growth for the majority of T&E species we monitored, especially at Kaʻūpūlehu Preserve, also highlight the importance of community involvement that both sites incorporate in their management goals. Culturally, these forests play

a critical role in educating the next generation not only in ecological and cultural knowledge of plant species but in the core significance of place and our responsibility to care for it. The continued conservation and preservation of these threatened and endangered forests has helped hold many stories of meaning and historical oral references that would have disappeared without the hard work and dedication to those who view these forests as more than just a group of trees.

Figures

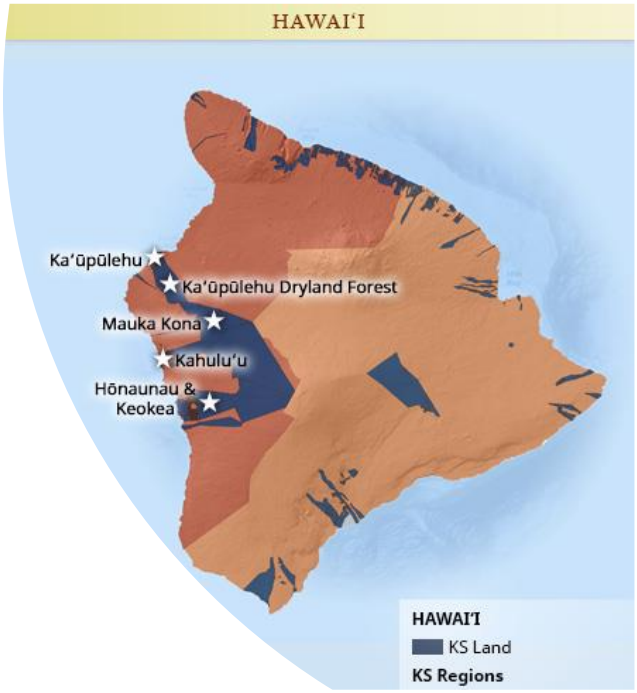


Figure 1.1. Map of Hawaiʻi Island and location of Kaʻūpūlehu Dryland Forest (Kamehameha Schools, 2014).

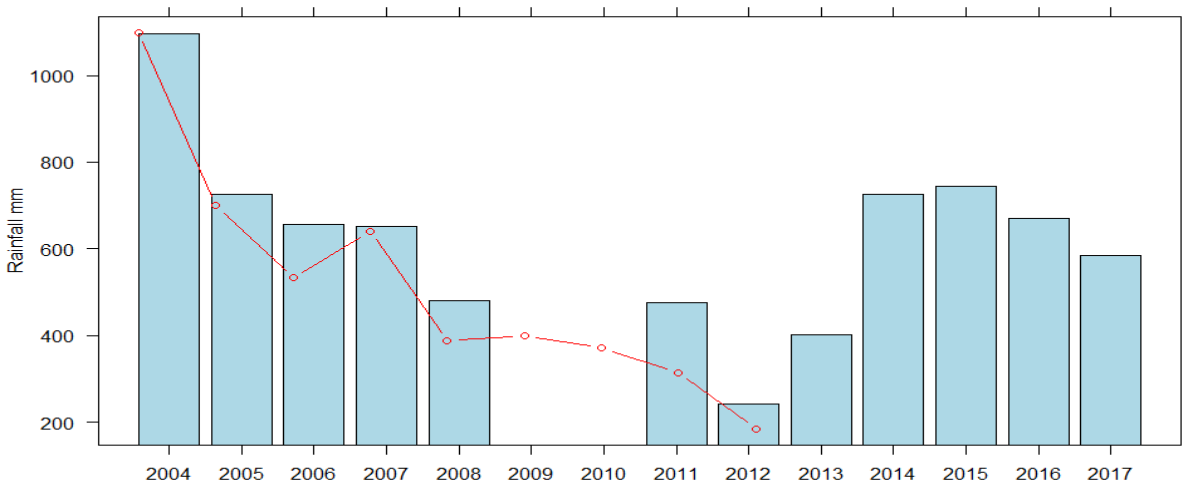


Figure 1.2. Annual rainfall (mm) from 2004 to 2017 recorded from Kaʻūpūlehu site (blue bars) and from the Hawaiʻi Rainfall Atlas, interpolated for Kaʻūpūlehu (red line). Kaʻūpūlehu data is missing for years 2009 and 2010. This study period for this research occurred from 2014 to 2017.

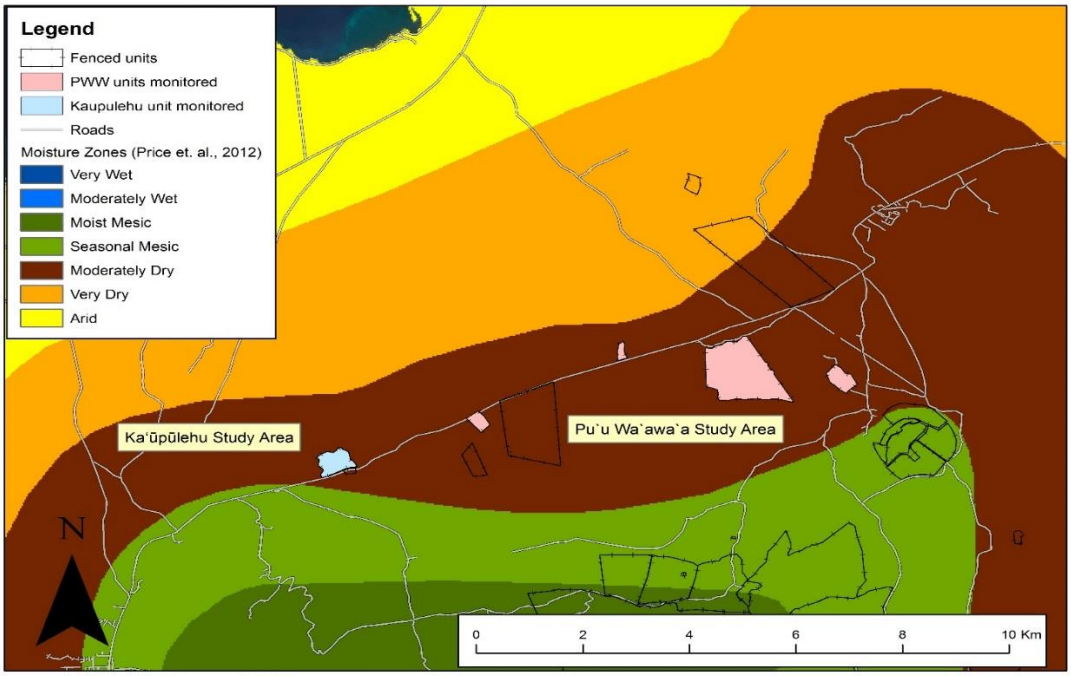


Figure 1.3. Moisture zones of Kaʻūpūlehu Preserve (blue) and Puʻu Waʻawaʻa Forest Reserve (pink) study sites (Pink). Created by Jim Jacobi, USGS.

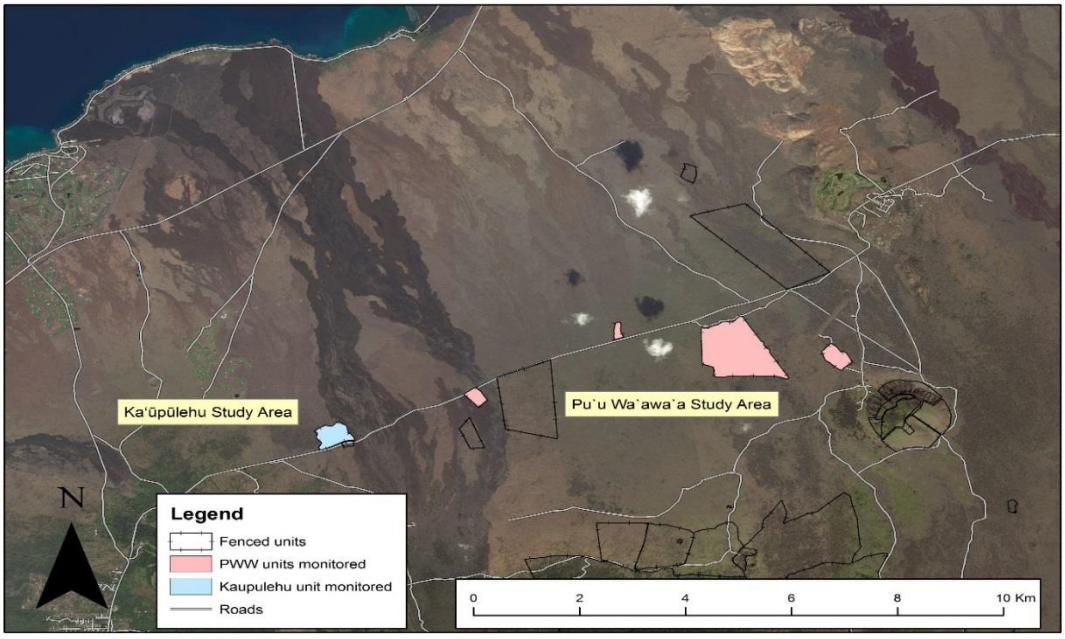


Figure 1.4. Map of Kaʻūpūlehu Study Site (Blue) and Puu waa waa Study Sites (Pink). Monitored units are colored. Created by Jim Jacobi, USGS.

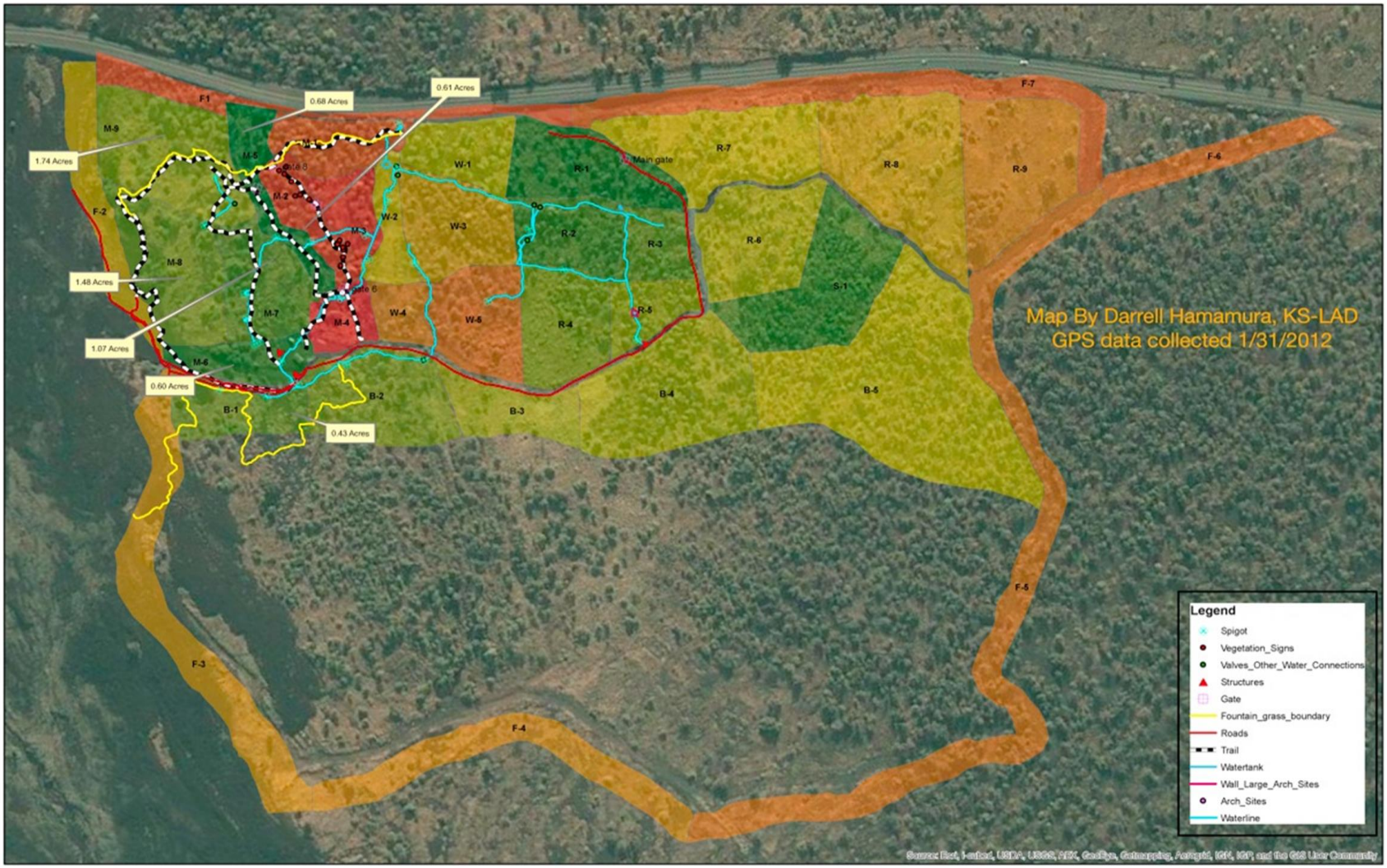


Figure 1.5. Map of zones in Ka'ūpūlehu Forest Preserve. The zones that we monitored for natural regeneration of threatened and endangered species are in color.

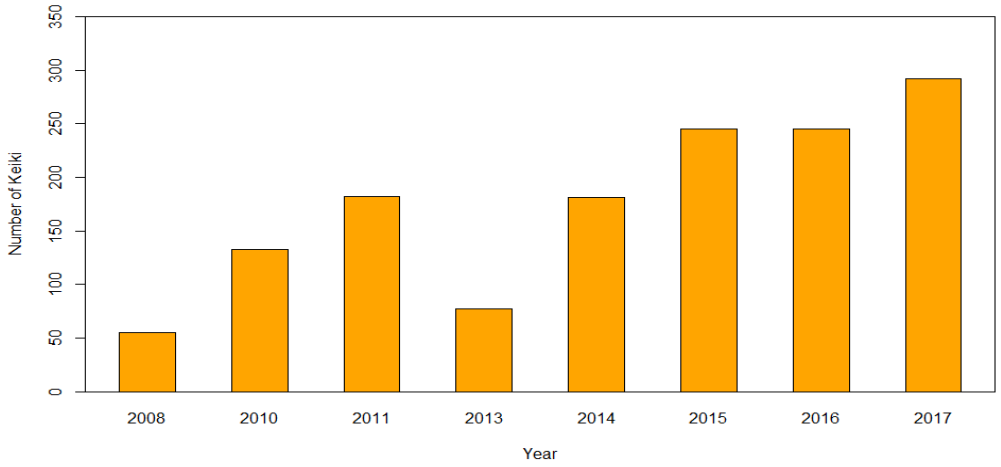


Figure 1.6a. Total number of naturally regenerated recruits (keiki) of 10 or our eleven T&E study species from 2013 to 2017. Koʻo koʻo lau is not included here because it had over 1000 naturally regenerated recruits.

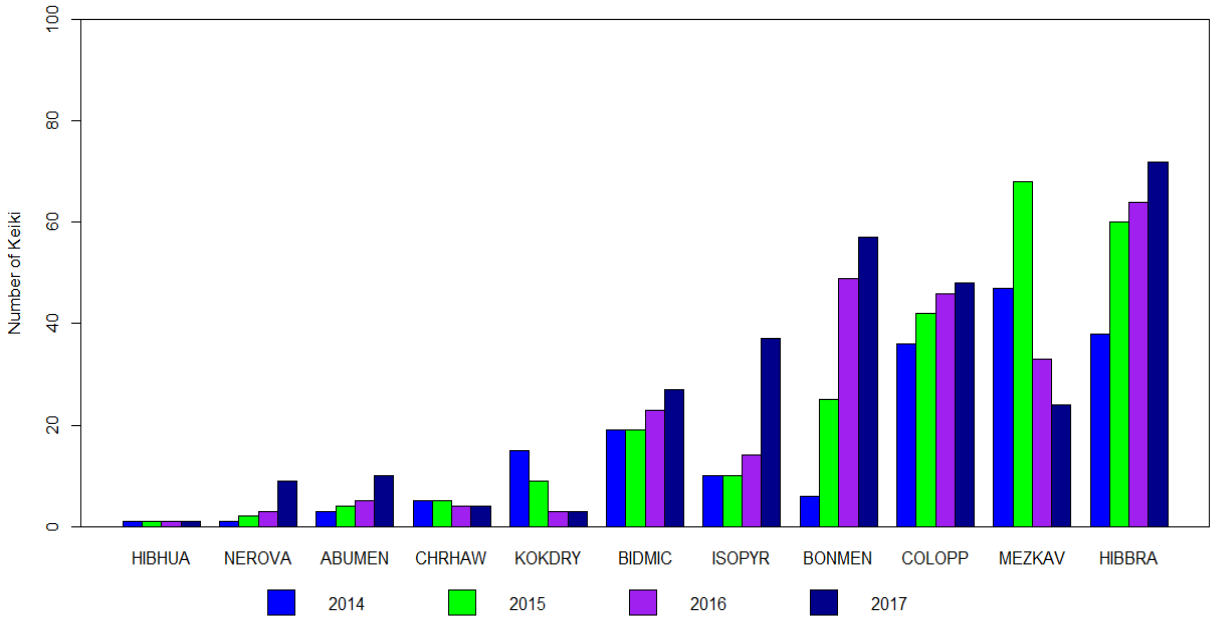


Figure 1.6b. Total number of naturally regenerated recruits (keiki) from 2014 to 2017 by species.
Code Names: HIBHUA – Hau kuahiwi, NEROVA – Maʻaloa, ABUMEN – Koʻo loa ʻula, CHRHAW – Halapepe, KOKDRY – Hau hele ʻula, BIDMIC – Koʻo koʻo lau, ISOPYR – Aupaka, BONMEN – Bonamia, COLOPP – Kauila, MEZKAV – Uhiuhi, HIBBRA – Maʻo hau hele.

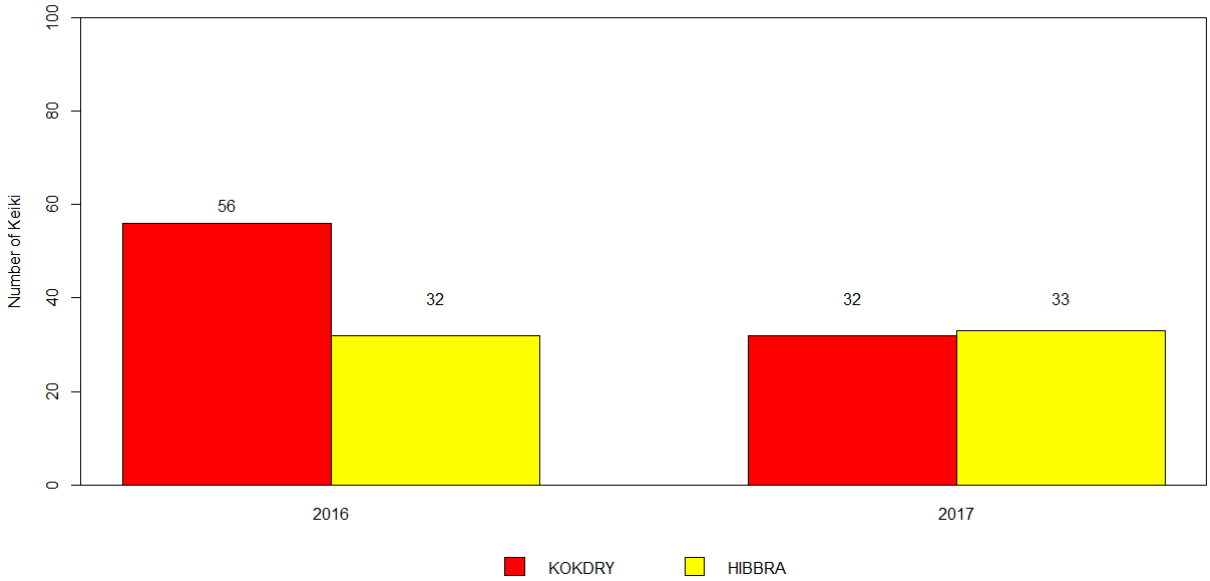


Figure 1.6c. Total number of naturally regenerated recruits (keiki) for (KOKDRY) Hau hele ʻula and (HIBBRA) Maʻo hau hele at four Puʻu Waʻawaʻa enclosures.

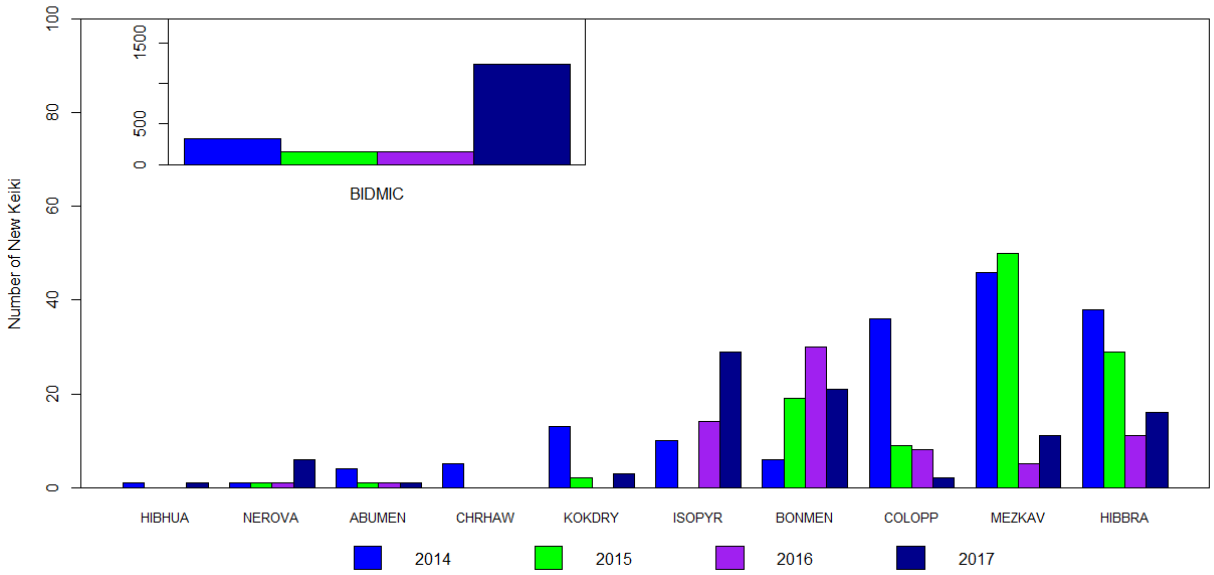


Figure 1.7a. Number of new naturally regenerated recruits appearing at each census from 2014 to 2017 in Kaʻūpūlehu Preserve.
Code Names: HIBHUA – Hau kuahiwi, NEROVA – Maʻaloa, ABUMEN – Koʻo loa ʻula, CHRHAW - Halapepe, KOKDRY – Hau hele ʻula, ISOPYR - Aupaka, BONMEN - Bonamia, COLOPP - Kauila, MEZKAV - Uhiuhi, HIBBRA – Maʻo hau hele, BIDMIC - Koʻo koʻo lau.

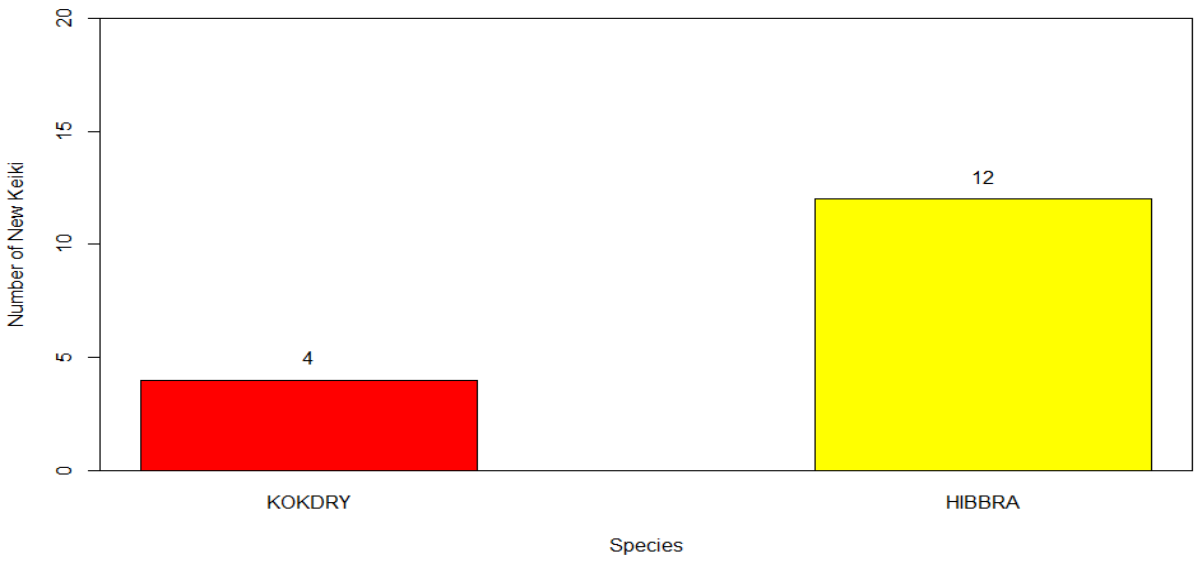


Figure 1.7b. Number of new naturally regenerated recruits found in 2017 for (KOKDRY) Hau hele ʻula and (HIBBRA) Maʻo hau hele in four Puʻu Waʻawaʻa enclosures.

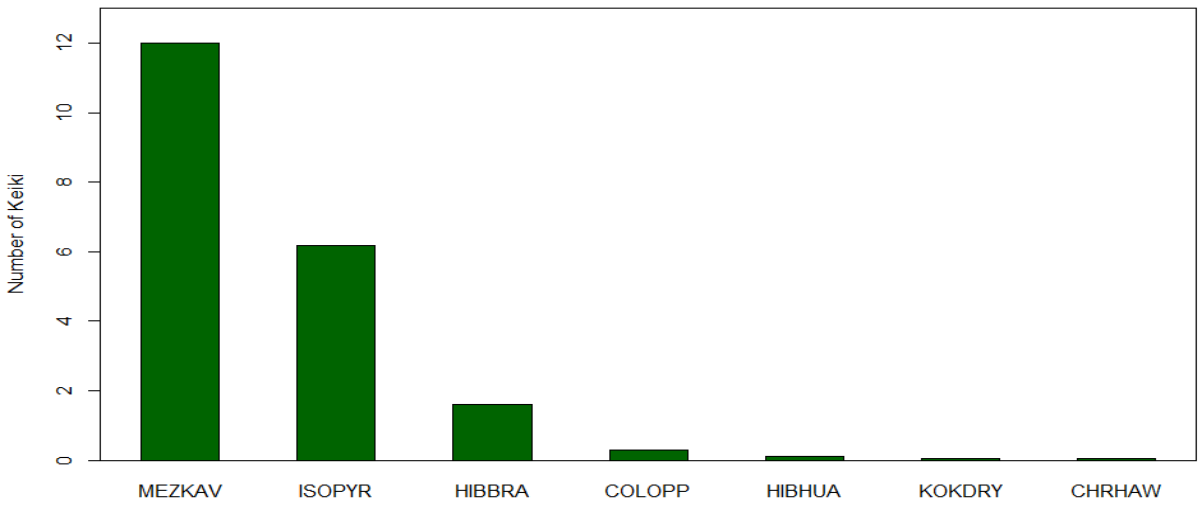


Figure 1.8. Number of new, naturally regenerated recruits in 2017, per reproductive adult present in Kaʻūpūlehu Preserve.
Code Names: MEZKAV - Uhiuhi, ISOPYR - Aupaka, HIBBRA – Maʻo hau hele, COLOPP - Kauila, HIBHUA – Hau kuahiwi, KOKDRY – Hau hele ʻula, CHRHAW – Halapepe.

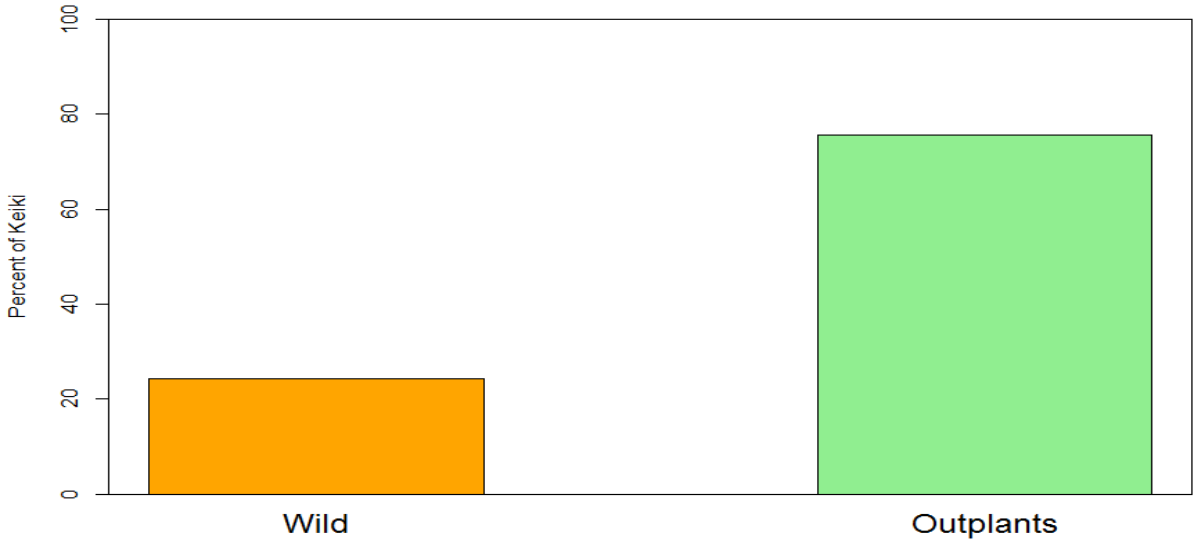


Figure 1.9a. Percentage of natural recruits that regenerated from wild versus outplanted sources, for all T&E species combined at Kaʻūpūlehu Preserve.

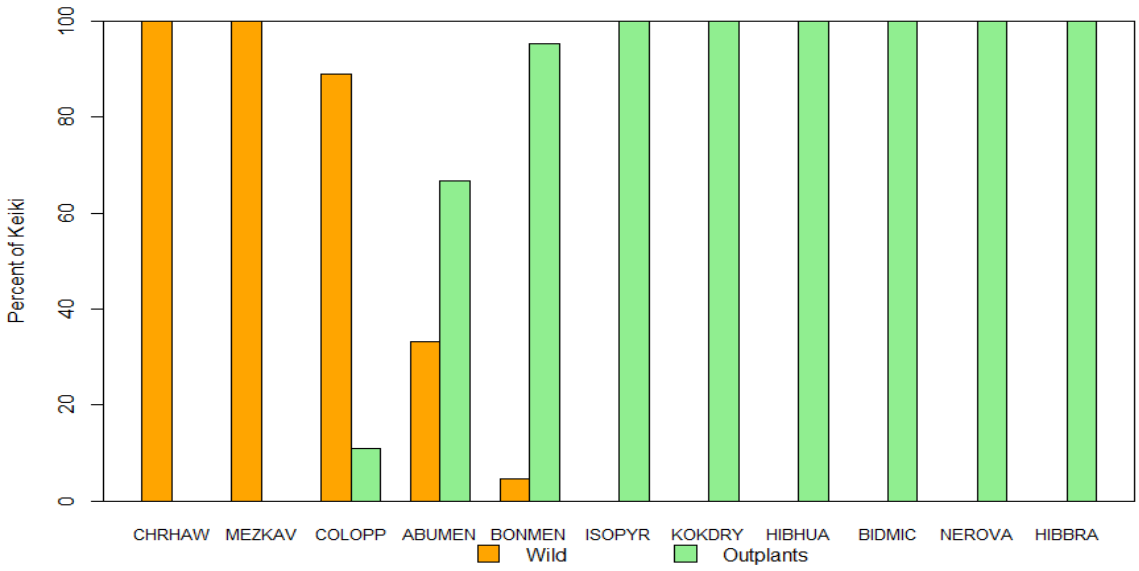


Figure 1.9b. Percentage of natural recruits that regenerated from wild versus outplanted sources for each species in 2017 in Kaʻūpūlehu Preserve.
Code Names: CHRHAW - Halapepe, MEZKAV - Uhiuhi, COLOPP - Kauila, ABUMEN – Koʻo loa ʻula, BONMEN - Bonamia, ISOPYR - Aupaka, KOKDRY – Hau hele ʻula, HIBHUA – Hau kuahiwi, BIDENS – Koʻo koʻo lau, NEROVA – Maʻaloa, HIBBRA – Maʻo hau hele.

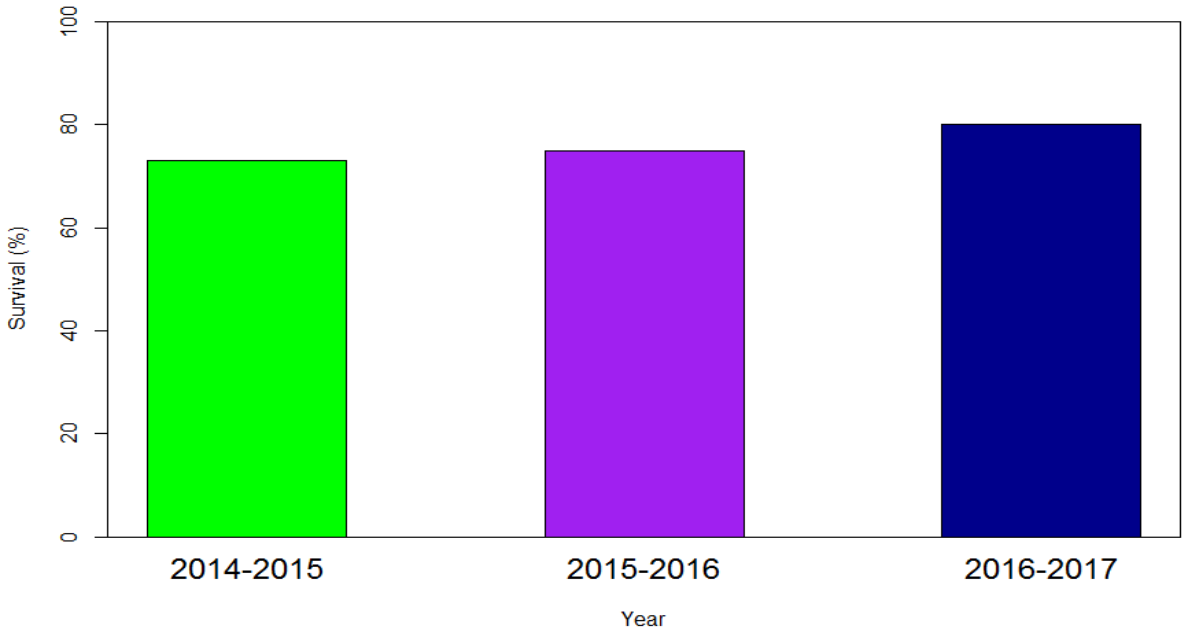


Figure 1.10a. Annual survival (%) of naturally recruited T&E species at Kaʻūpūlehu Preserve, from 2014 to 2017.

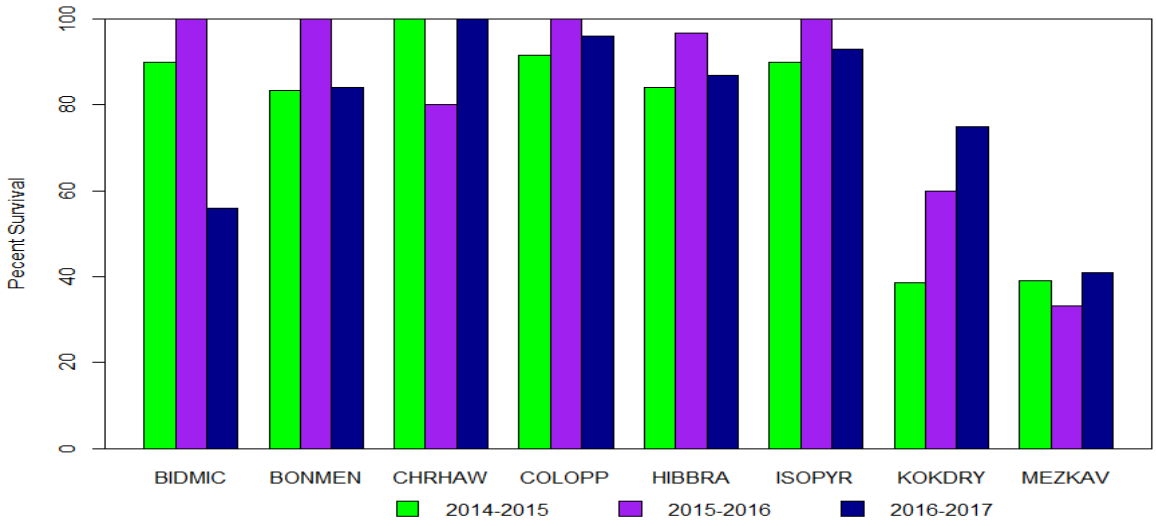


Figure 1.10b. Annual survival (%) of natural recruits, by species, Kaʻūpūlehu Preserve, from 2014 to 2017

Code Names: BIDENS – Koʻo koʻo lau, BONMEN - Bonamia, CHRHAW - Halapepe, COLOPP - Kauila, HIBBRA – Maʻo hau hele, ISOPYR - Aupaka, KOKDRY – Hau hele ʻula, MEZKAV - Uhiuhi.

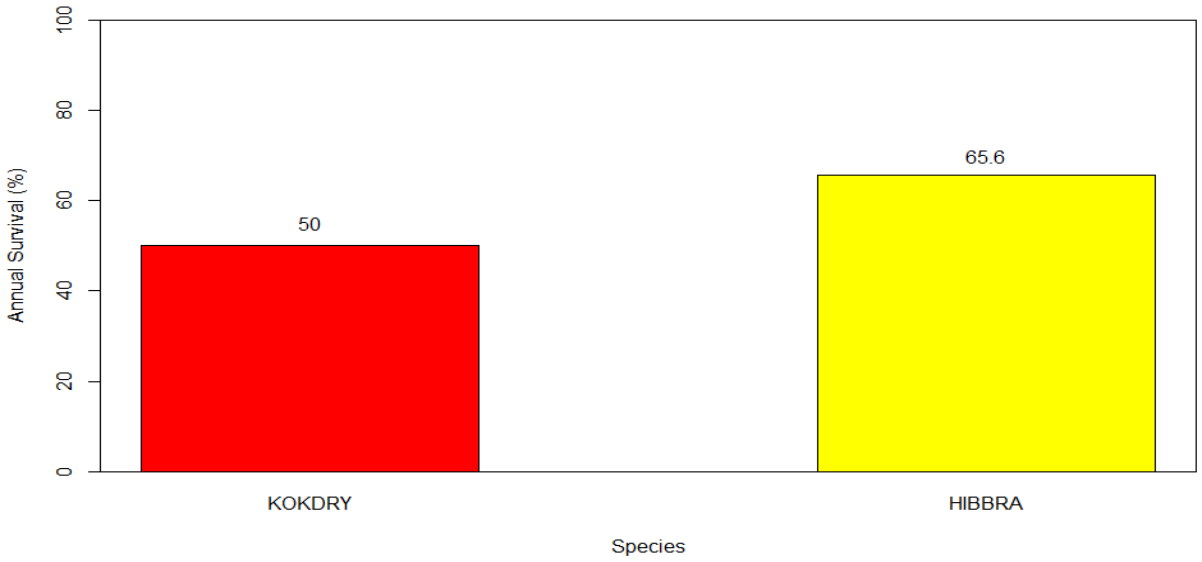


Figure 1.10c. Annual of survival (Aug 2016 to Aug 2017) for (KOKDRY) Hau hele ʻula and (HIBBRA) Maʻo hau hele natural recruits, in four enclosures at Puʻu Waʻawaʻa.

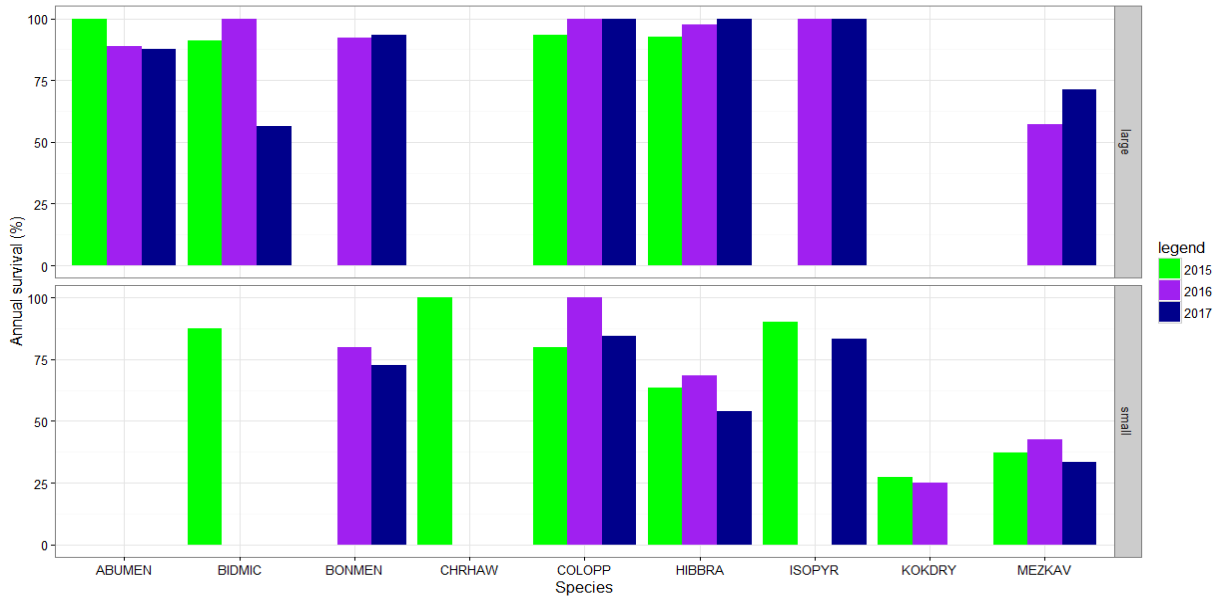
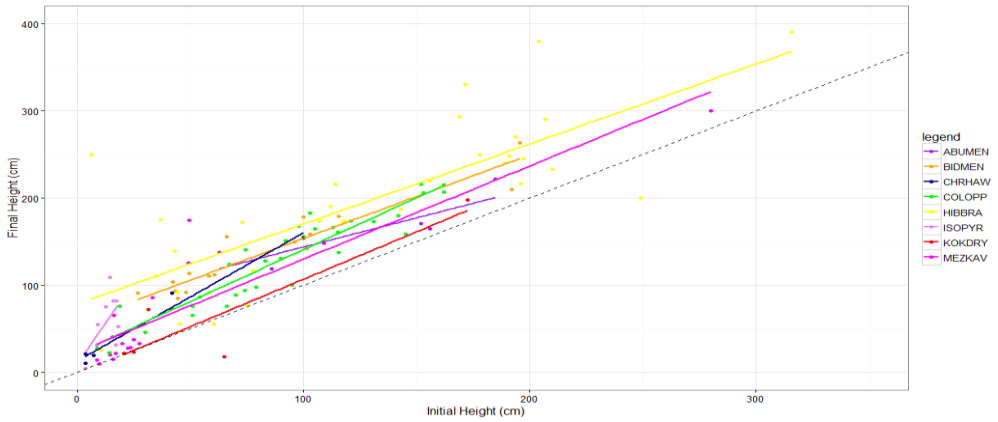
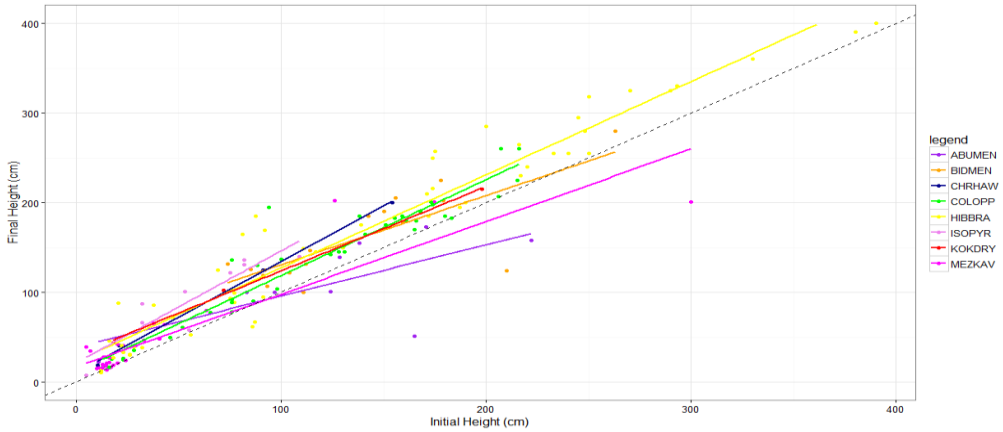


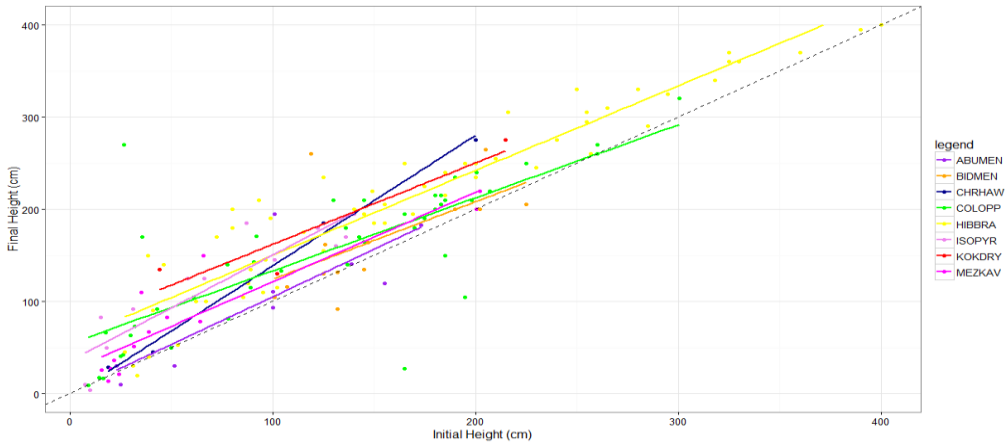
Figure 1.10d. Annual survival (%) of natural recruits at Kaʻūpūlehu Preserve, from 2014 to 2017. Small recruits are <50cm high, large are >=50cm high. Species with <4 individuals for any given year and size-class were omitted.
Code Names: ABUMEN – Koʻo loa ʻula, BIDMIC – Koʻo koʻo lau, BONMEN - Bonamia, CHRHAW - Halapepe, COLOPP - Kauila, HIBBRA – Maʻo hau hele, ISOPYR - Aupaka KOKDRY – Hau hele ʻula, MEZKAV – Uhiuhi.



a) 2014-2015



b) 2015-2016



c) 2016-2017

Figure 1.11a. Annual growth in height natural recruits at Kaʻūpūlehu Preserve for a) 2014-2015 b) 2015-2016 and c)2016-2017. The dotted line represents zero growth. Species with less than five individuals were not included.
Code Names: ABUMEN – Koʻo loa ʻula, BIDMEN – Koʻo koʻo lau, CHRHAW - Halapepe, COLOPP - Kauila, HIBBRA – Maʻo hau hele, ISOPYR - Aupaka, KOKDRY – Hau hele ʻula, MEZKAV – Uhiuhi.

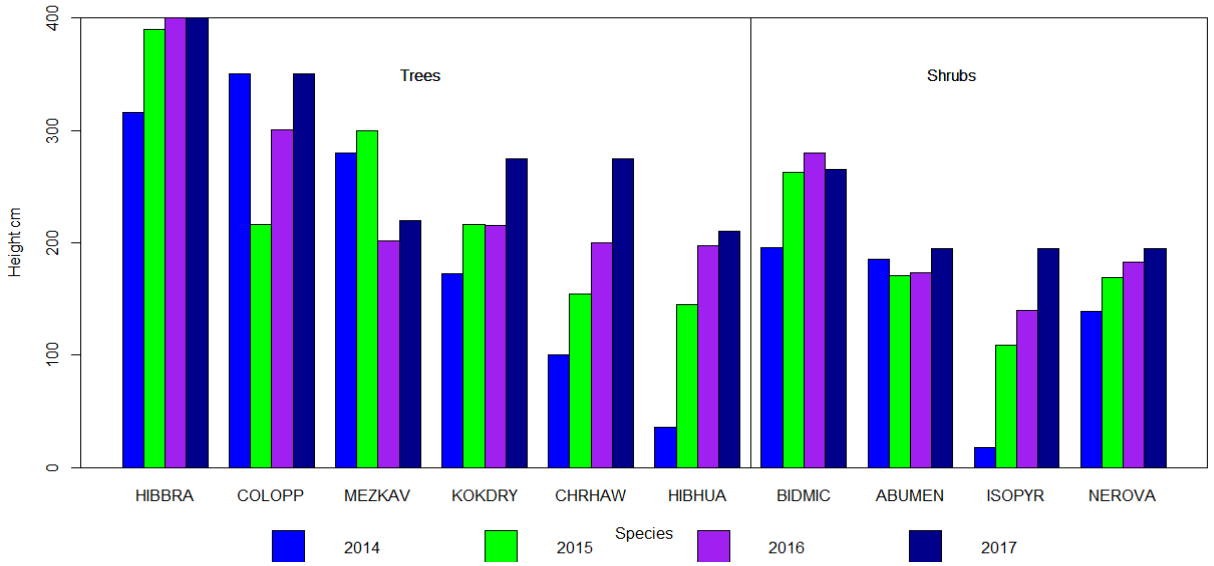


Figure 1.11b. Height of the tallest natural recruits by species Kaʻūpūlehu Preserve from 2014 to 2017.
Code Names: HIBBRA – Maʻo hau hele COLOPP - Kauila, MEZKAV - Uhiuhi, KOKDRY – Hau hele ʻula, CHRHAW – Halapepe, HIBHUA – Hau kuahiwi, BIDMIC – Koʻo koʻo lau, ABUMEN – Koʻo loa ʻula, ISOPYR - Aupaka, NEROVA – Maʻaloa.

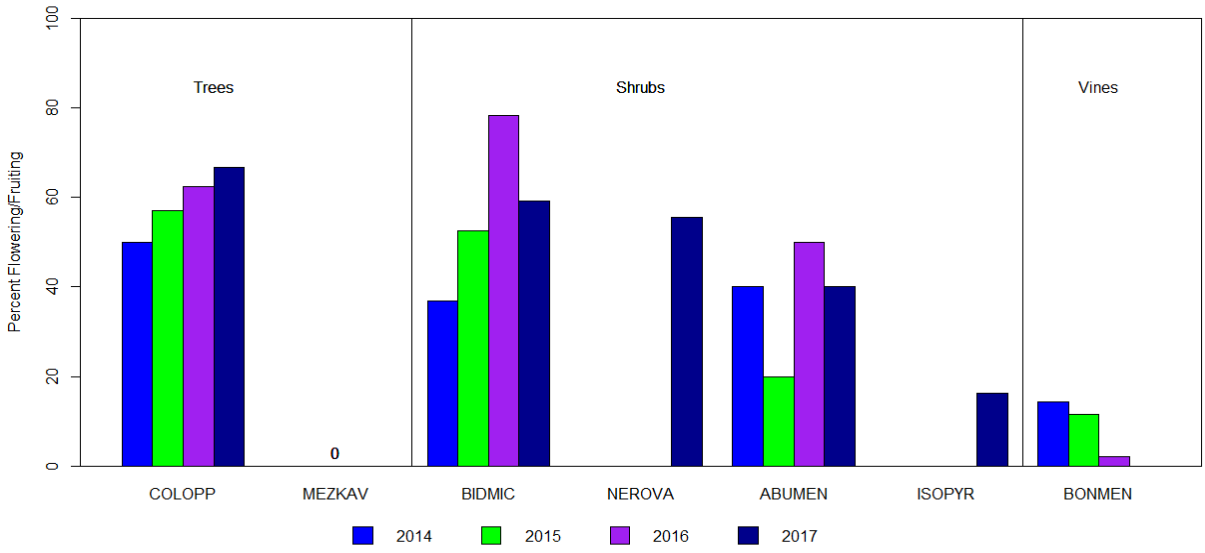


Figure 1.12. Percentage of regenerated recruits Kaʻūpūlehu Preserve that flowered or fruited in each December from 2014 to 2017 for each species. Species that flower or fruit in the spring are not included.
Code Names: COLOPP - Kauila, MEZKAV - Uhiuhi, BIDMIC – Koʻo koʻo lau, NEROVA – Maʻaloa, ABUMEN – Koʻo loa ʻula, ISOPYR - Aupaka, BONMEN – Bonamia.

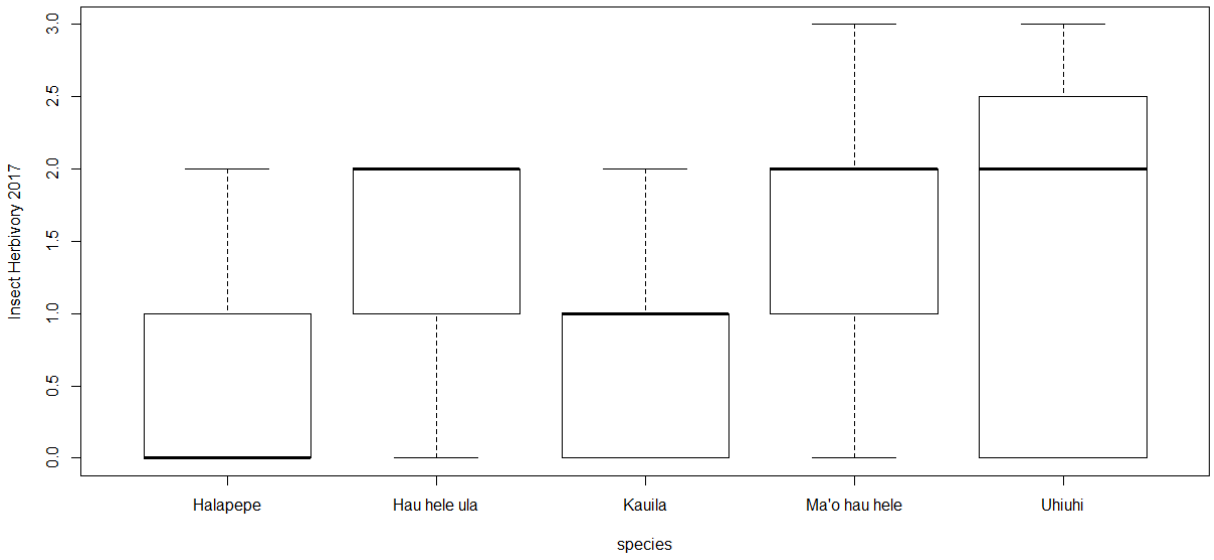


Figure 2.1. Level (ranked) of insect herbivory intensities (0-3) across species in Kaʻūpūlehu Preserve.

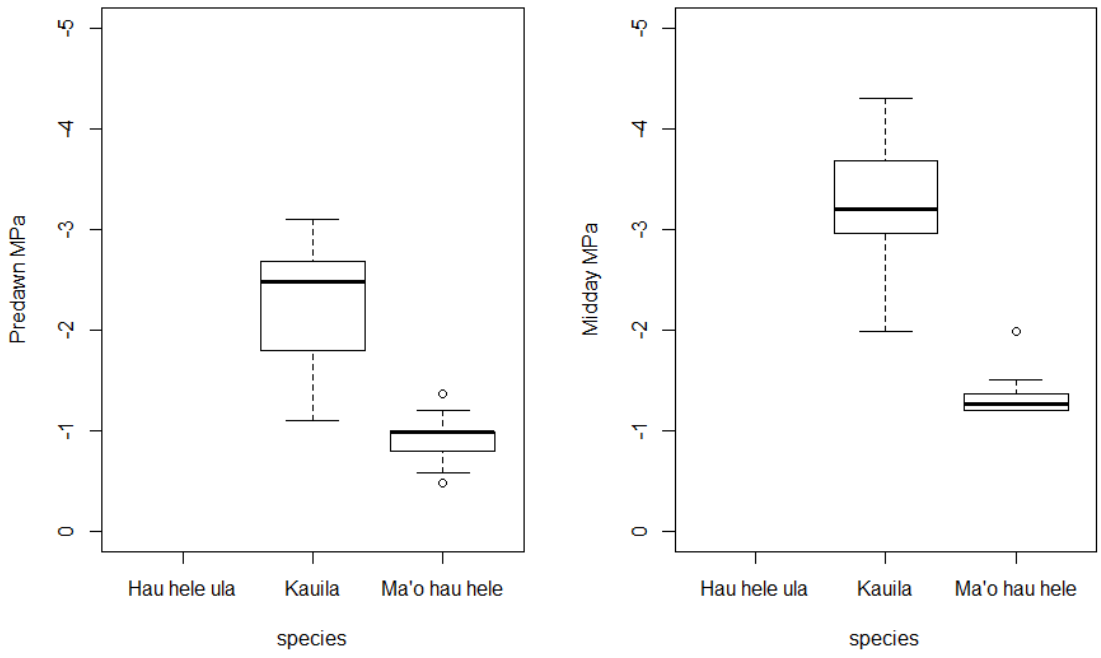


Figure 2.2. Summer (July) water potential (predawn and midday) across species in Kaʻūpūlehu Preserve.

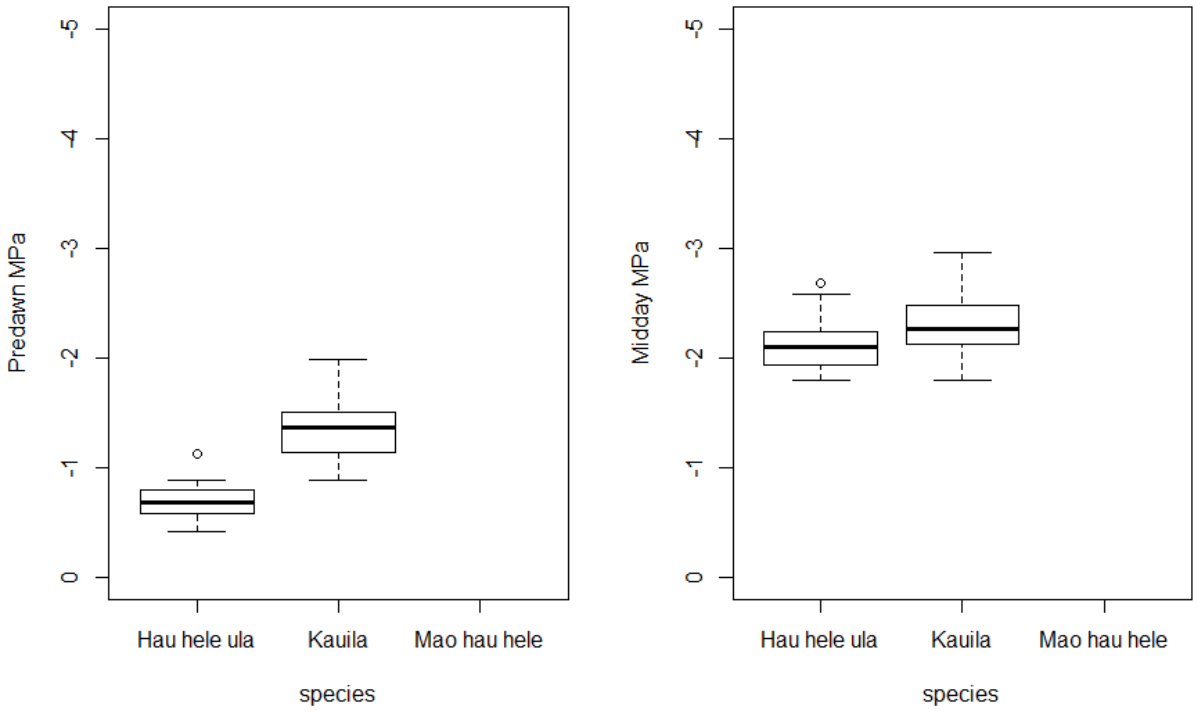


Figure 2.3. Winter (December) water potential (predawn and midday) across species in Kaʻūpūlehu Preserve.

Appendix

Table 1: Number of natural **r**ecruits for T&E species in Kaʻūpūlehu Preserve (See Figure 6b).

Species	2014	2015	2016	2017
AUPAKA	10	10	14	37
BONAMIA	6	25	49	57
HALAPEPE	5	5	4	4
HAU HELE ʻULA	15	9	3	3
HAU KUAHIWI	1	1	1	1
KAUILA	36	42	46	48
KOʻO KOʻO LAU	19	19	23	27
KOʻOLOAʻULA	3	4	5	10
MAʻALOA	1	2	3	9
MAʻO HAU HELE	38	60	64	72
UHIUHI	47	68	33	24
Total	**181**	**245**	**245**	**292**

Table 2: Number of new natural recruits found at each annual census in Kaʻūpūlehu Preserve (See Figure 7a).

Species	2014	2015	2016	2017
AUPAKA	10	0	14	84
BONAMIA	6	19	30	21
HALAPEPE	5	0	0	0
HAU HELE ʻULA	13	2	0	3
HAU KUAHIWI	1	0	0	1
KAUILA	36	9	8	2
KOʻOKOʻOLAU	324	161	156	1246
KOʻOLOAʻULA	4	1	1	1
MAʻALOA	1	1	1	6
MAʻO HAU HELE	38	29	11	16
UHIUHI	46	50	5	11
Total	**484**	**272**	**226**	**1391**

References

Allen, William. (2000). Bioscience: Restoring Hawai'i's Dry Forests. American Institute of Biological Sciences 50.12(1037). Web. 11 Mar 2011. Pages 17-18. http://web.ebscohost.com/src/pdf?vid=2&hid=101&sid=1986e991-e978-408b-96f8-8b6635e2bd31%40sessionmgr104.

Allison, A. (2003). Biological surveys–new perspectives in the Pacific. Organisms Diversity & Evolution, 3(2), 103-110.

Athens JS, Tuggle HD, Ward JV, Welch DJ (2002). Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i. Archaeology Ocean 37, 57–78.

Athens, J. S. (2009). *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. Biological Invasions 11:1489 – 1501.

Banko, W.E. and P.C. Banko. (2009). Historic decline and extinction. Pgs. 25-58 In Pratt, T.K., C. T. Atkinson, P.C. Banko, J.D. Jacobi, and B. Woodworth (edition.), Hawaiian Forest Birds: Their Biology and Conservation. Yale University Press, New Haven CT.

Barton, K. E., & Hanley, M. E. (2013). Seedling–herbivore interactions: insights into plant defense and regeneration patterns. Annals of Botany, 112(4), 643-650.

Basset, Y. (1991). Influence of leaf traits on the spatial distribution of insect herbivores associated with an overstorey rainforest tree. Oecologia, 87(3), 388-393.

Blackmore, M., and P. M. Vitousek. (2000). Cattle grazing, forest loss, and fuel loading in a dry forest ecosystem at Pu'u Wa'awa'a Ranch, Hawai'i. Biotropica 32:625 – 632.

Blumenthal, D., Mitchell, C. E., Pyšek, P., & Jarošík, V. (2009). Synergy between pathogen release and resource availability in plant invasion. Proceedings of the National Academy of Sciences, 106(19), 7899-7904.

Brooks, T. M., S. L. Pimm & N. J. Collar. (1997). Deforestation predicts the number of threatened birds in insular Southeast Asia. Conservation Biology, 11: 383-394.

Brooks, S., S. Cordell, and L. Perry. (2009). Broadcast seeding as a potential tool to reestablish native species in degraded dry forest ecosystems in Hawai'i. Ecology Restoration, 27:300 – 305.

Brown, S., Lugo, A. E. (1982). The Storage and Production of Organic Matter in Tropical Forests and Their Role in in the Global Carbon Cycle. Biotropica. 4(3), 161-187.

Bruegmann, M. M. (1996). Hawai'i's dry forests. Endangered Species Bulletin 11:26–27.

Bullock, S. H., Mooney, H. A., & Medina, E. (Editors.). (1995). Seasonally dry tropical forests. Cambridge University Press.

Bullock, S. H., H. A. Mooney & E. Medina (Editors). (1996). Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Cabin, R. J., S. G. Weller, D. H. Lorence, S. Cordell, L. J. Hadway, R. Montgomery, D. Goo, and A. Urakami. (2002). Effects of light, alien grass, and native species additions on Hawai'ian dry forest restoration. Ecology Application, 12:1595 – 1610.

Cabin, R.J., S. G. Weller, D. H. Lorence., S. Cordell, L. J. Hadway. (2001). Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve. Elsevier: Biological Conservation, 104:181-190.

Cabin, R. J., S. G. Weller, D. H. Lorence, T. W. Flynn, A. K. Sakai, D. Sandquist, and L. J. Hadway. (2000). Effects of longterm ungulate exclusion and recent alien species control on the preservation and restoration of a Hawai'ian tropical dry forest. Conservation Biology, 14:439–453.

Cal Poly Pomona (CPP). (2012). Dracaena konaensis (Asparagaceae) – halapepe. Website. Retrieved from http://www.cpp.edu/~ejquestad/hawaiipropguide/Dracaena%20konaensis.html.

Ceccon, E., Huante, P., and Rincón, E. (2006). Abiotic Factors Influencing Tropical Dry Forests Regeneration. Brazilian Archives of Biology and Technology. 49(2), 305-312.

Chimera, C. G., and D. R. Drake. (2010). Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. Biotropica 42:493 – 502.

Chimera, C. G., and D. R. Drake. (2011). Could poor seed dispersal contribute to predation by introduced rodents in a Hawai'ian dry forest? Biological Invasions, 13:1029–1042.

Cole, F. R., Loope, L. L., Medeiros, A. C., Raikes, J. A., & Wood, C. S. (1995). Conservation Implications of Introduced Game Birds in High‐Elevation Hawaiian Shrubland. Conservation Biology, 9(2), 306-313.

Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. Annual review of ecology and systematics, 27(1), 305-335.

Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological monographs, 53(2), 209-234.

Conry, P. J. (2010). Hawai'i statewide assessment of forest conditions and trends: Prepared by RJ Cannarella. Accessed online March 12, 2013.

Cordell, S., Cabin, R. J., Weller, S. G., & Lorence, D. H. (2002). Simple and cost-effective methods control fountain grass in dry forests (Hawai'i). Ecological Restoration, 20, 139-140.

Cordell, S. McClellan, M. Yarber, Y. C. and Hadway, L. J. (2008). Towards restoration of Hawai'ian tropical dry forests: the Kaupulehu outplanting programme. Pacific Conservation Biology. 14: 279–284.

Cordell, S., Ostertag, R., Rowe, B., Sweinhart, L., Vasquez-Radonic, L., Michaud, J., Cole, C.T., Schulten, J.R. (2009). Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. Elsevier: Biological Conservation, 142:2997–3004.

Cordell, S., Sandquist, D.R. (2008). The impact of an invasive African bunch grass (Pennisetum setaceum) on water availability and productivity of canopy trees within a tropical dry forest in Hawai'i. Functional Ecology, 22: 1008-1017.

Cowling, R. M., & Hilton Taylor, C. (1994). Patterns of plant diversity and endemism in southern Africa: an overview. Botanical diversity in southern Africa. Strelitzia, 1, 31-52.

Crone, E., Menges, E., Ellis, M., Bell, T., Bierzychudek, P., Ehrlen, J., Kaye, T., Knight, T., Lesica, P., Morris, W., Oostermeijer, G., Quintana-Ascencio, P., Stanley, A., Ticktin, T., Valverde, T., and Williams, J. (2011). How do plant ecologists use matrix population models? Ecology Letters 14(1),1-8.

Cuddihy, L. W., and C. P. Stone. (1990). Alteration of native Hawaiian vegetation: Effects of humans, their activities and introductions. Cooperative National Park Resources Studies Unit, University of Hawai'i at Manoa, Honolulu.

D'Antonio, C. M., Hughes, R. F., Mack, M., Hitchcock, D., & Vitousek, P. M. (1998). The response of native species to removal of invasive exotic grasses in a seasonally dry Hawai'ian woodland. Journal of Vegetation science, 9(5), 699-712.

D'Antonio, C. M., and P. M. Vitousek. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review Ecology Systematics, 23:63 – 87.

Denslow, J. S., Uowolo, A. L., & Hughes, R. F. (2006). Limitations to seedling establishment in a mesic Hawaiian forest. Oecologia, 148(1), 118-128.

Foster, RB (1982) The seasonal rhythm of fruit fall on Barro Colorado Island. In: Leigh EG Jr, Rand AS, Windsor DM (Editors). The ecology of a tropical forest. Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC, 151–172.

Foster, J. T., & Robinson, S. K. (2007). Introduced birds and the fate of Hawaiian rainforests. Conservation Biology, 21(5), 1248-1257.

Franks, S. J., Kral, A. M., & Pratt, P. D. (2006). Herbivory by introduced insects reduces growth and survival of Melaleuca quinquenervia seedlings. Environmental entomology, 35(2), 366-372.

Frazier, A. G. and Giambelluca, T. W. (2017). Spatial trend analysis of Hawaiian rainfall from 1920 to 2012 International Journal of Climatology, 37,2522–3155.

Friday, J.B., Cordell, S., Giardina, C.P, Inman-Narahari, F., Koch, N., James J. K. Leary, J.J.K., Litton, C.M., Trauernicht, C. (2015). Future Directions for Forest Restoration in Hawai'i. New Forests. 46:733–746.

Funk, J. L., & Throop, H. L. (2010). Enemy release and plant invasion: patterns of defensive traits and leaf damage in Hawai'i. Oecologia, 162(4), 815-823.

Garwood, N. (1982). Seasonal rhythm of seed germination in a semideciduous tropical forest. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes, 173-185.

Gemma, J. N., Koske, R. E., and Habte, M. (2002). Mycorrhizal Dependency of Some Endemic and Endangered Hawai'ian Plant Species. American Journal of Botany, 89(2): 337–345.

Gentry, Alwyn H., edition. (1993). Four neotropical rainforests. Yale University Press.

Gerhardt, K. (1996). Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. Forest Ecology and Management, 82(1-3), 33-48.

Gerhardt, K. and Hytteborn, H. (1992). Natural dynamics and regeneration methods in tropical dry forests - an introduction. Journal of Vegetation Science, 3: 361-364.

Giambelluca, T.W., Q. Chen, A.G. Frazier, J.P. Price, Y.-L. Chen, P.-S. Chu, J.K. Eischeid, and D.M. Delparte, (2013): Online Rainfall Atlas of Hawai'i. Bulletin of the American Meteorological Society, 94, 313-316, doi: 10.1175/BAMS-D-11-00228.1.

Giffin, J.G. (1993). New species of fossil birds found at Puu Wa'awa'a. Elepaio, 53, 1–3.

Gillespie, T. W., Keppel, G., Pau, S., Price, J. P., Jaffré, T., Meyer, J. Y., & O'Neill, K. (2011). Floristic composition and natural history characteristics of dry forests in the Pacific. Pacific Science, 65(2), 127-141.

Gillespie, R. G., & Roderick, G. K. (2002). Arthropods on islands: colonization, speciation, and conservation. Annual review of entomology, 47(1), 595-632.

Gordon, D. R., Menke, J. M., & Rice, K. J. (1989). Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. Oecologia, 79(4), 533-541.

Greco, E. B., & Wright, M. G. (2015). Ecology, biology, and management of *Xylosandrus compactus* (Coleoptera: Curculionidae: Scolytinae) with emphasis on coffee in Hawai'i. Journal of Integrated Pest Management, 6(1).

Gregg, R.M., editor. (2018). Hawaiian Islands Climate Vulnerability and Adaptation Synthesis. EcoAdapt, Bainbridge Island, WA.

Griffin, Jon G. (2003). Pu‘u Wa‘awa‘a Biological Assessment. State of Hawai’i Department of Land and Natural Resources Division of Forestry and Wildlife.

HFIA. (2007). Hawai’i’s Dryland Forests. Hawai’i Forest Industry Association. Web. 11 March 2011. http://www.Hawai’iforest.org/reports/dryland.html

Imbert, D. and Portecop, J. (2008). Hurricane disturbance and forest resilience: Assessing structural vs. functional change s in a Caribbean dry forest. Forest Ecology and Management, 255:3494–3501.

Innes, J., W. G. Lee, B. Burns, C. CampbellHunt, C. Watts, H. Phipps, and T. Stephens. (2012). Role of predator-proof fences in restoring New Zealand’s biodiversity: A response to Scofield et al. New Zealand. Journal of Ecology, 36:232 – 238.

Jacobi, J. D., & Warshauer, F. R. (1992). Distribution of six alien plant species in upland habitats on the island of Hawai’i. Alien plant invasions in native ecosystems of Hawai’i. Cooperative National Park Resources Studies Unit, University of Hawai’i, Honolulu, 155-188.

Jahn, C. Gary & W Beardsley, John. (2018). Interactions of Ants (Hymenoptera: Formicidae) and Mealybugs (Homoptera: Pseudococcidae) on Pineapple. Proceedings of the Hawaiian Entomology Society, 34:161–165.

Janzen, D. (1988). Tropical dry forests. The most endangered major tropical ecosystem. E. O. Wilson, edition. Biodiversity. National Academy of Sciences/Smithsonian Institution, Washington, D.C. 130 – 137.

Janzen, D. (1986). The Future of Tropical Ecology. Annual Review of Ecology and Systematics, 17:305-324.

Joe, S. M., & Daehler, C. C. (2008). Invasive slugs as under-appreciated obstacles to rare plant restoration: evidence from the Hawaiian Islands. Biological Invasions, 10(2), 245-255.

Kamehameha Schools. (2014). Natural and Cultural Resources Management. Our Land Kuleana. Map Used. Website. http://www.ksbe.edu/land/lad_crm_wh/

Kauahikaua, J., Cashman, K.V., Clague, D.A., Champion, D., Hagstrum, J.T. (2002). Emplacement of the most recent lava flows on Hualalai Volcano, Hawai‘i. Bulletin of Volcanology, 64:229–253.

Kern, C. C., Reich, P. B., Montgomery, R. A., & Strong, T. F. (2012). Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? Forest Ecology and Management, 267, 134-143.

King, S. P., & Roth, R. W. (2006). Broken Trust: Greed, Mismanagement, and Political Manipulation at America's Largest Charitable Trust. University of Hawai'i Press.

Kirika, J., Farwig, N., & Bohning - Gaese, K. A. T. R. I. N. (2008). Effects of Local Disturbance of Tropical Forests on Frugivores and Seed Removal of a Small‐Seeded Afrotropical Tree. Conservation Biology, 22(2), 318-328.

Krist, F. J. (2014). 2013-2027 National insect and disease forest risk assessment. United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team.

Litton, C. M., D. R. Sandquist, and S. Cordell. (2006). Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest in Hawai'i. Forest Ecology Management, 231:105–113.

Loiselle, B. A., & Blake, J. G. (2002). Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Seed dispersal and frugivory: ecology, evolution and conservation. CABI, Wallingford, UK, 397-405.

Loope LL (1998) Hawai'i and the Pacific Islands. In: Mac MJ, Opler PA, Puckett Haecker CE, Doran PD (Editors). Status and trends of the nation's biological resources. US Geological Survey, 747–774.

Maza-Villalobos, S., Balvanera, P., and Mart´ınez-Ramos, M. (2011). Early Regeneration of Tropical Dry Forest from Abandoned Pastures: Contrasting Chrono sequence and Dynamic Approaches. Biotropica, 43(6): 666–675.

McAuliffe, S., Martinez, J. I. M. (2015). Herbivory and arthropod diversity within invaded and native forest types on Hawai'i Island. Journal of Young Investigators. 29(5).

Medeiros, A. C., and E. I. von Allmen. (2006). Restoration of native Hawaiian dryland forest at Auwahi, Maui. U.S. Geological Survey Fact Sheet, 2006 – 3035.

Medeiros, A. C., C. F. Davenport, and C. G. Chimera. (1998). Auwahi: Ethnobotany of a Hawa'ian dryland forest. Cooperative National Park Resources Studies Unit, University of Hawai'i at Mänoa, Department of Botany. Pacific Cooperative Study Unit Technology, 117.

Medeiros, A. C., Loope, L. L., & Cole, F. R. (1986). Distribution of ants and their effects on endemic biota of Haleakala and Hawai'i Volcanoes National Parks: a preliminary assessment.

Meyer, J.-Y., and J.-F. Butaud. (2009). The impacts of rats on the endangered native flora of French Polynesia (Pacific islands): Drivers of plant extinction or coup de grace species? Biological Invasions 11:1569 – 1585.

Miles, L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. E. Gordon. (2006). A global overview of the conservation status of tropical dry forests. J. Biogeography. 33:491 – 505.

Miller, P. M. (1999). Effects of deforestation on seed banks in a tropical deciduous forest of western Mexico. Journal of Tropical Ecology, 15(2), 179-188.

Murphy, P. G., Ariel E. Lugo. (1986). Ecology of Tropical Dry Forest. Annual Review of Ecology and Systematics, 17: 67-88.

Offenberg, J. (2001). Balancing between mutualism and exploitation: the symbiotic interaction between Lasius ants and aphids. Behavioral Ecology and Sociobiology, 49(4), 304-310.

Olson, D. D., and Dinerstein, E. (2002). The Global 200: Priority Ecoregions for Global Conservation. Annals of the Missouri Botanical Garden, 89:199-224.

Olson, S. L., & James, H. F. (1982). Fossil birds from the Hawai'ian Islands: evidence for wholesale extinction by man before western contact. Science, 217(4560), 633-635.

Olson, S. L., & James, H. F. (1991). Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part I. Non-Passeriformes. Ornithological Monographs, (45), 1-88.

Parker III, T. A., and J. L. Carr, editors. (1992). Status of forest remnants in the Cordillera de la Costa and adjacent areas of south- western Ecuador. Conservation International, Washington, D.C.

Parker, T. A, Gentry, A. H., Foster, R. B., Emmons, L. H., and Remsen, J. V. (1993). The lowland dry forests of Santa Cruz, Bolivia: a global conservation priority. Conservation International, Rapid Assessment Program, RAP working papers no. 4, Washington, DC.

Pau, S., T. W. Gillespie, and J. P. Price (2009), Natural history, biogeography, and endangerment of Hawaiian dry forest trees, Biodiversity in Conservation, 18, 3167–3182.

Perkins, K. S., Nimmo, J. R., & Medeiros, A. C. (2012). Effects of native forest restoration on soil hydraulic properties, Auwahi, Maui, Hawaiian Islands. Geophysical Research Letters, 39(5).

PMS Instrument Company. (2018). Interpreting Data. Website. Retrieved from https://www.pmsinstrument.com/resources/interpreting-data.

Pratt HD, Bruner PL, Berrett DG. (1987). The birds of Hawai'i and the tropical Pacific. Princeton University Press, Princeton.

Pratt, L.W. and J.D. Jacobi. (2009). Loss, degradation, and persistence of habitats. In Pratt, T.K., C. T. Atkinson, P.C. Banko, J.D. Jacobi, and B. Woodworth (Editors), Hawaiian Forest Birds: Their Biology and Conservation. Yale University Press, New Haven CT. 137-158.

Price, J. P., Gon III, S. M., Jacobi, J. D., & Matsuwaki, D. (2007). Mapping plant species ranges in the Hawaiian Islands: Developing a methodology and associated GIS layers.

Raven, P. H. (1988). Our diminishing tropical forests. In E. O. Wilson (editor), Biodiversity. National Academy, Washington, D.C. 199-122.

Reaka-Kudla, M. L., D. E. Wilson & E. O. Wilson (editors). (1997). Biodiversity II: Understanding and Protecting our Biological Resources. Joseph Henry Press, Washington, D.C.

Rico‐Gray, V., & García‐Franco, J. G. (1992). Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. Journal of vegetation science, 3(5), 617-624.

Rock, J. F. (1913). The indigenous trees of the Hawaiian Islands. Reprinted in 1974 by Pacific Tropical Botanical Garden, La¯wa‘i, Kaua‘i, Hawai‘i, and Charles F. Tuttle, Rutland, Vermont.

Rodríguez-Cabal, M. A., Aizen, M. A., & Novaro, A. J. (2007). Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America. Biological Conservation, 139(1-2), 195-202.

Sabogal, C. (1992). Regeneration of tropical dry forests in Central America, with examples from Nicaragua. Journal of vegetation science, 3(3), 407-416.

Sakai, A. K., W. L. Wagner, and L. A. Mehrhoff. (2002). Patterns of endangerment in the Hawai’ian flora. Systematics of Biology, 51:276–302.

Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., ... & Fajardo, L. (2005). Research priorities for neotropical dry forests. Biotropica, 37(4), 477-485.

Sandquist, D. R., & Cordell, S. (2007). Functional diversity of carbon-gain, water-use, and leaf-allocation traits in trees of a threatened lowland dry forest in Hawaii. American Journal of Botany, 94(9), 1459-1469.

Schulten, J. R., Cole, T. C., Cordell, S., Publico, K. M., Ostertag, R., E. Enoka, J., & Michaud, J. D. (2014). Persistence of native trees in an invaded Hawaiian lowland wet forest: experimental evaluation of light and water constraints. Pacific Science, 68(2), 267-285.

Skoglund, J. (1992). The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. Journal of vegetation Science, 3(3), 357-360.

Soriana, A. & Sala, O.E. (1983) Ecological strategies in a Patagonian arid steppe Vegetation, 56, 9–15.

Stratton, L., Hudson, L., Suenaga, N. and Morgan, B., (1998). Overview of Hawai'ian dry forest c propagation techniques. Newsletter of the Hawai'ian Botanical Society, 13–27.

Styrsky, D. John and Micky D. Eubanks. (2007). Ecological consequences of interactions between ants and honeydew-producing insects. Proceedings of the Royal Society Biological Sciences, 274, 151–164.

Sujatnika, J. P., T. R. Soehartono, M. J. Crosby & A. Mardiastuti. (1995). Conserving Indonesian Biodiversity: The Endemic Bird Area Approach. Bird Life International Indonesia Programme, Bogor, Indonesia.

Swaine, M. D. (1992). Characteristics of dry forest in West Africa and the influence of fire. Journal of vegetation science, 3.3:365-374.

Thaxton, J.M., Cordell, S., Cabin, R.J., Sandquist, D.R. (2012). Non-Native Grass Removal and Shade Increase Soil Moisture and Seedling Performance during Hawai'ian Dry Forest Restoration. Restoration Ecology, 20(4), 475-482.

Thaxton, J. M., Cole, T. C., Cordell, S., Cabin, R. J., Sandquist, D. R., and Litton, C. M. (2010). Native Species Regeneration Following Ungulate Exclusion and Nonnative Grass Removal in a Remnant Hawai'ian Dry Forest. Pacific Science, 64(4), 533–544.

Traveset, A., & Richardson, D. M. (2006). Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution, 21(4), 208-216.

Wagner, W. L., Herbst, D. R., & Sohmer, S. H. (1999). Manual of the Flowering Plants of Hawai'i, University of Hawai'i and Bishop Museum Press. 1&2(2).

WCMC. (1992). Global Biodiversity: Status of the Earth's Living Resources. Chapman and Hall, London.

Weller, S.G., Cabin, R.J., Lorence, D.H., Perlman, S., Wood, K., Flynn, T., and Sakai, A.K. (2011). Alien Plant Invasions, Introduced Ungulates, and Alternative States in a Mesic Forest in Hawai'i. Restoration Ecology, 19(5), 671–680.

Wilmshurst, J. M., Hunt, T. L., Lipo, C. P., & Anderson, A. J. (2011). High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. Proceedings of the National Academy of Sciences, 108(5), 1815-1820.

Wilson, E. O. (1992). The Diversity of Life. Belknap Press, Cambridge, Massachusetts.

Wilson, E. O. (editor). (1988). Biodiversity. National Academy Press, Washington, D.C.

Willson, M. F., & Traveset, A. (2000). The ecology of seed dispersal. Seeds: The ecology of regeneration in plant communities, 2:85-110.

Winn, M. F., Lee, S. M., & Araman, P. A. (2013). Forest Crowns: A software tool for analyzing ground-based digital photographs of forest canopies. In Proceedings, 18th central hardwood forest conference, 35-41.

Wikramanayake, E., E. Dinerstein, C. Loucks, D. Olson, J. Morrison, J. Lamoreux, M. McKnight & P. Hedao. (2001). Terrestrial Ecoregions of the Indo-Pacific: A Conservation Assessment. Island Press, Washington, D.C.

Wright, T.L., Chun, J.Y.F., Esposo, J., Heliker, C., Hodge, J., Lockwood, J.P., and Vogt, S.M. (1992). Map Showing Lava Flow Hazard Zones, Island of Hawai'i. Miscellaneous Field Studies Map. MF-2193. USGS.

WWF/IUCN. (1997). Centers of Plant Diversity: A Guide and Strategy for their Conservation. IUCN Publications Unit, Cambridge, U.K, 3.

Zhang, D. Y., & Jiang, X. H. (2006). Interactive effects of habitat productivity and herbivore pressure on the evolution of anti-herbivore defense in invasive plant populations. Journal of theoretical biology, 242(4), 935-940.

Zhou, A., Zeng, L., Lu, Y., Xu, Y., & Liang, G. (2012). Fire ants protect mealybugs against their natural enemies by utilizing the leaf shelters constructed by the leaf roller, *Sylepta derogata*. Plos one, 7(11), e49982.